



A University of Sussex PhD thesis

Available online via Sussex Research Online:

<http://sro.sussex.ac.uk/>

This thesis is protected by copyright which belongs to the author.

This thesis cannot be reproduced or quoted extensively from without first obtaining permission in writing from the Author

The content must not be changed in any way or sold commercially in any format or medium without the formal permission of the Author

When referring to this work, full bibliographic details including the author, title, awarding institution and date of the thesis must be given

Please visit Sussex Research Online for more information and further details



DOCTORAL THESIS

**Bodily and Affective Shared
Self-Other Representations in
Vicarious Pain Responders**

*A thesis submitted in fulfilment of the requirements
for the degree of Doctor of Philosophy*

Author:

Vanessa Elena Botan

Date:

August 2020

I, Vanessa Elena Botan, hereby declare that this thesis has not been and will not be submitted in whole or in part to another university for the award of any other degree.

Brighton,
August 2020

Vanessa Elena Botan

ACKNOWLEDGEMENTS

Firstly, I would like to express my sincere gratitude to my supervisor Prof. Jamie Ward for the continuous support provided throughout my Ph.D study and related research, for his vast knowledge, experience, and precious advice. His guidance was extremely valuable, and I could have not completed my PhD without his support.

I would also like to thank my second supervisor, Prof. Hugo Critchley, for his insightful comments, for giving me access to research facilities and for all the help provided throughout this PhD.

My sincere gratitude also goes to Dr. Charlotte Rae, Dr. Warrick Roseboom, Dr David Schwartzman, and Prof Anil Seth for stimulating discussions, for helping me setting up experiments, and for their insightful comments on my research. Without their precious support it would have not been possible to conduct this research.

Last but not the least, I would like to thank my family, my partner, and my friends for supporting me emotionally throughout my PhD.

AUTHOR CONTRIBUTION

This thesis is written in an ‘article format’ and comprises four empirical chapters which were written for publication in peer reviewed journals. The first and last chapters represent the introduction and discussion of the entire research undertaken as part of this thesis and a link between the four empirical chapters. I am the principal author on **Articles I & III** which have already been published and **Articles II & IV** which will be submitted for publication. I take responsibility for the design, data collection and analysis, and write-up of this research. Prof Jamie Ward is the senior author on **Articles I & III** to reflect his expertise and contribution to all the stages of the research constituting these two articles. Prof Hugo Critchley is the co-author on **Articles I & III** to reflect his supervision during the write-up of these articles. Miss Fan is credited in Article I for her help with data collection and experimental design. Prof Banissy and Dr Bowling are also credited in **Article III** for their contributions to the write-up of the final manuscript.

Article I is published in *Consciousness and Cognition* as:

Botan, V., Fan, S., Critchley, H., & Ward, J. (2018). Atypical susceptibility to the rubber hand illusion linked to sensory-localised vicarious pain perception. *Consciousness and cognition*, 60, 62-71.

Article III is published in *Frontiers in Psychology* as:

Botan, V., Bowling, N. C., Banissy, M., Critchley, H., & Ward, J. (2018). Individual Differences in Vicarious Pain Perception Linked to Heightened Socially Elicited Emotional States. *Frontiers in psychology*, 9, 2355.

University of Sussex
School of Psychology
Sackler Centre for Consciousness Science

DOCTORAL THESIS

Bodily and Affective Shared Self-Other Representations in Vicarious Pain Responders

by Vanessa Elena Botan

SUMMARY

Vicarious pain responses represent the ability to mirror the physical pain of others on our own bodies, a phenomenon that has been linked to individual differences in multi-sensory processing and empathic traits. There is considerable inter-individual variability in the quality of the pain felt and previous research individuated two groups of people, constituting about 30% of the population, that consciously report feeling the physical pain of others on their own bodies. The two groups are distinguished by the quality of the pain felt: one group reports localised and sensorial qualities (S/L group) whilst the other one reports generalised and affective qualities (A/G group). Vicarious pain perception is intrinsically linked to the body and evidence suggests that differences in bodily phenotypes shape the sensorial and/or affective perception of pain. This thesis further investigated both exteroceptive and interoceptive bodily processes which may be linked to the different qualities of vicarious pain experience.

The first three studies of this thesis tested the prediction that vicarious pain responders may have greater bodily malleability and a general tendency to treat all other bodies

as related to themselves. The central paradigm used in these studies was the rubber hand illusion (RHI), a measure of how much participants are predisposed to feel that an extraneous body part (i.e. a dummy hand) belongs to them. **Article I** demonstrated that sensory-localised vicarious pain responders (S/L) perform atypically on the task and are more susceptible to the illusion in the asynchronous and light conditions. **Article II** further explored why the RHI is not disrupted by asynchrony in the S/L group by applying models of Bayesian sensory inference which explain greater susceptibility to RHI illusion through stronger precision of certain sensory modalities (e.g. vision, touch). The Enfacement Illusion (EI) was also employed in this study as a second paradigm in order to further clarify the role of proprioception in bodily awareness. The overall results re-confirmed that S/L responders perceive asynchrony as synchrony, mainly because they rely more on rhythmic expectations and are more susceptible to proprioceptive imprecision.

Article III further addressed the tendency of vicarious pain responders to identify with others, but this time at a social-cognitive level. It employed a series of empathy questionnaires and a self-other association task. The results of vicarious pain responders were comparable to controls on most measures. There were no differences in the social self-other association task and neither on other measures of cognitive empathy such as perspective taking or social skills. Notably, both sensory and affective aspects of vicarious pain were associated with higher emotional contagion and reactivity but not with higher levels of personal distress suggesting that they may have better emotional regulation. **Article IV** further investigated the results of **Article III** by recording physiological reactivity including skin conductance, blood pressure and heart rate variability (HRV) (a measure of emotion regulation) in vicarious pain responders as well as interoceptive processing. The findings showed that the affective-general responders have lower interoceptive accuracy whilst the sensory-localised responders have higher emotion regulation. They provided evidence for differences in interoceptive accuracy and emotion regulation which distinguished between the sensory and affective groups.

Taken together, the findings of this thesis further characterise bodily and self-other processes in vicarious pain responders and provide substantial evidence for differences in the exteroceptive domain associated with the sensory quality of vicarious pain and differences in the interoceptive domain associated with the affective quality of pain.

Contents

List of Figures	xii
List of Tables	xiv
1 Introduction	1
1.1 Vicarious pain perception	1
1.1.1 Vicarious pain perception: a general overview.	1
1.1.2 Vicarious pain questionnaire and qualities of vicarious pain.	4
1.2 Theories of vicarious pain perception.	5
1.2.1 Core trauma and chronic pain as precursors for vicarious pain.	5
1.2.2 Enhanced mirroring activity in vicarious pain perception.	8
1.2.3 Mirroring activity and activation of simulation mechanisms in vicarious pain perception.	10
1.3 Shared self-other representations in vicarious pain responders: the link with empathy.	11
1.3.1 Shared bodily representations in vicarious pain perception. Bodily ownership: the rubber hand illusion and enfacement illu- sion paradigms.	14 15
1.3.2 Shared affective representations in vicarious pain responders.	18
1.4 Aims	20
2 Article I: Atypical Susceptibility to the Rubber Hand Illusion linked to Sensory-Localised Vicarious Pain Perception	22

2.1	Abstract	22
2.2	Introduction	24
2.3	Materials and methods	28
2.3.1	Participants	28
2.3.2	Vicarious Pain Questionnaire	28
2.3.3	Rubber Hand Illusion Questionnaire	29
2.3.4	Experimental procedure	30
2.3.5	Data Analysis	31
2.4	Results	32
2.4.1	Reliability of the VPQ	32
2.4.2	Proprioceptive drift	33
2.4.3	Subjective ratings	35
2.5	Discussion	36
2.5.1	Previous atypical findings in the RHI	37
2.5.2	Theoretical models explaining the RHI	39
2.6	Conclusion	41
3	Article II: Atypical susceptibility to the Rubber Hand Illusion and Enfacement Illusion in Sensory-Localised Vicarious Pain Responders. Evidence for greater influence of tactile-temporal predictions.	42
3.1	Abstract	42
3.2	Introduction	43
3.2.1	Bodily ownership. An overview of the rubber hand illusion (RHI) and enfacement illusion (EI) paradigms	43
	Rubber Hand Illusion	43
	Enfacement Illusion	46
3.2.2	Bodily ownership and vicarious pain	47
3.3	Materials and Methods	51
3.3.1	Participants	51
3.3.2	Vicarious Pain Questionnaire (VPQ)	52
3.3.3	Rubber Hand Illusion	52
3.3.4	Enfacement illusion (EI)	53
3.3.5	Data analysis	55

3.4	Results	57
3.4.1	RHI proprioceptive drift results	57
3.4.2	RHI Subjective ratings	61
3.4.3	EI: Point of Subjective Equality (PSE) results	62
3.4.4	EI: Subjective ratings	63
3.5	Discussion	64
3.5.1	RHI results and the Bayesian Sensory Inference Model	65
3.5.2	EI results	67
3.5.3	General Conclusions	69
4	Article III: Individual Differences in Vicarious Pain Perception Linked to Heightened Socially Elicited Emotional States	70
4.1	Abstract	70
4.2	Introduction	72
4.3	Materials and methods	75
4.3.1	Participants	75
4.3.2	Measures	76
	Vicarious Pain Questionnaire	76
	Emotional Contagion Scale	77
	Empathy Quotient	77
	Interpersonal Reactivity Index	77
	Helping Attitudes Scale	78
	The Individualism – Collectivism Interpersonal Assessment In- ventory (ICIAI)	78
	Self-Other Association Task	78
4.3.3	Procedure	79
4.3.4	Statistical Analyses	79
4.4	Results	80
4.4.1	Between Group Differences: One-Way ANOVAs	80
4.4.2	Between Group Differences: Factor Analysis and MANOVAs	80
4.4.3	Self-Other Associations	82
4.5	Discussion	84
4.5.1	Socially Elicited Emotional States	84

4.5.2	Low Emotion Regulation	85
4.5.3	Interpersonal and Imaginary Abilities	86
4.5.4	Self-Other Associations	87
4.5.5	Summary	87
5	Article IV: Differences in Interoceptive Accuracy and Emotion Regulation Distinguish between Affective and Sensory aspects of Feeling the Pain of Others	89
5.1	Abstract	89
5.2	Introduction	91
5.2.1	Vicarious Pain Responders: General Introduction	91
5.2.2	Bodily self and interoceptive awareness in vicarious pain responders	92
5.2.3	Bodily and emotional processing in vicarious pain responders	94
5.3	Materials and Methods	97
5.3.1	Participants	97
5.3.2	Vicarious Pain Questionnaire	98
5.3.3	Interoceptive Accuracy and Awareness	98
5.3.4	Psychophysiological responses to vicarious pain	99
5.3.5	Physiological Measures	99
	Heart Rate and Heart Rate Variability	99
	Blood Pressure	100
	Skin Conductance Response	100
5.3.6	Anxiety Questionnaire. State-Trait Anxiety Inventory (STAI)	100
5.3.7	Statistical Data Analyses	101
5.4	Results	103
5.4.1	Interoceptive accuracy and awareness	103
5.4.2	Heart Rate (HR) and Heart Rate Variability (HRV)	103
5.4.3	Blood Pressure	104
5.4.4	Skin Conductance	105
5.4.5	Anxiety Results and Trait measures correlations	105
5.4.6	Hierarchical Multiple Regression Models for main outcome variables	106

5.5	Discussion	111
5.5.1	Summary of Results	111
5.5.2	Interoceptive processes	112
5.5.3	Anxiety, HRV and Emotion Regulation	115
5.5.4	Physiological Arousal: SBP and SCR	117
6	Discussion	119
6.1	Summary of Findings	119
6.2	Methodological limitations and future directions	125
6.3	Contributions to the field and present theories	131
6.4	General Conclusions	133
	Bibliography	135
A	Appendix A: Supplementary Materials for Article I	162
A.1	VPQ group differences comparing TPRs with intensity	162
A.2	Baseline comparisons and non-parametric tests	162
A.3	Percentages of people experiencing the illusion in each group	163
B	Appendix B: Supplementary Materials for Article II	165
B.1	RHI and EI questionnaire items	165
B.2	RHI entire sample analyses	165
B.2.1	Proprioceptive drift results	165
B.2.2	Questionnaire results	167
	Ownership	167
	Location	167
	Agency	167
B.2.3	Correlation analyses between drift and subjective ratings	168
B.2.4	Differences in proprioceptive imprecision depending on the pre- ceding condition	168
B.3	Collapsing results for drift in the synchronous and asynchronous condi- tions	169
C	Appendix C: Supplementary Materials for Article III	170
C.1	Non-parametric tests results.	170

C.2	Effect sizes	170
D	Appendix D: Supplementary Materials for Article IV	172
D.1	Non-parametric tests results	172

List of Figures

1.1	An example of an accident video presented in the VPQ and a series of questions assessing various qualities of pain such as intensity and localisation. . .	5
1.2	A schematic representation of Fitzgibbon and colleagues model of vicarious pain. Taken from Fitzgibbon et al. (2010b)	6
1.3	A schematic representation of the RHI paradigm indicating the incoming sensory signals including vision, touch and proprioception.	16
1.4	The set-up of the Enfacement Illusion paradigm. The image was taken from Tajadura-Jimenez et al. (2011)	18
2.1	Mean PDs (mm) of the three groups for Synchronous and Asynchronous conditions. Error bars indicate one standard error.	34
2.2	Mean PDs (mm) of the three groups for the Light condition. Error bars indicate one standard error.	35
2.3	Subjective ratings in the asynchronous condition for each sub-scale.	36
2.4	Subjective ratings in the synchronous condition for each sub-scale	36
3.1	EI task: detailed representation.	55
3.2	Proprioceptive drift in the synchronous and asynchronous conditions in each group. Bars indicate the mean \pm 1 standard error. Non-R= controls; S/L= sensory-localised; A/G= affective-general.	58

3.3	Proprioceptive drift in a) vision-only condition against synchronous and asynchronous conditions; b) asynchronous-random condition against synchronous and asynchronous conditions. Bars indicate the mean \pm 1 standard error. Non-R= controls; S/L= sensory-localised; A/G= affective-general. . . .	59
3.4	a) Proprioceptive imprecision at baseline expressed in mm; b) correlation between proprioceptive imprecision at baseline and drift in the asynchronous condition; c) correlation between proprioceptive imprecision at baseline and drift in vision-only condition.	60
3.5	PSE for synchronous and asynchronous conditions in each group. Bars indicate the mean \pm 1 standard error. Non-R= controls; S/L= sensory-localised; A/G= affective-general.	62
4.1	IRI, EQ, ECS, and HAS scores. S/L, sensory-localised; A/G, affective-general. Both S/L and A/G scored higher on emotional contagion (ECS) and emotional reactivity (EQ-ER) than controls but not on cognitive empathy (EQ-CE) or social skills (EQ-SS) subscales. No significant differences were found on IRI and HAS. Error bars indicate \pm 1 SE. ($p < 0.05$)	81
4.2	ICIAI and self-other association task results. S/L, sensory-localised; A/G, general affective. The effects of closeness appear both in subjective scores and in task reaction times but not as an effect of group. All groups show a similar trend in RTs to the self-other association. Error bars indicate \pm 1 SE.	83
5.1	a) Recording set-up and interface; b) Task set-up.	101
5.2	Interoceptive accuracy and awareness scores. Error bars indicate $\pm 1SE$. * $p < 0.01$	103
5.3	Heart Rate (HR) at resting state as beats per minute (BPM) and during the task as beats per 10s video (BPV) for each pain category and control in the upper part of the figure. Heart rate variability (HRV) as RMSSD expressed in milliseconds (ms) at resting state and during the task in the lower part of the figure. Main effect of group for task HRV with S/L group having higher HRV than controls. Error bars indicate $\pm 1SE$. * $p < 0.05$	104

5.4	Mean systolic blood pressure and skin conductance results. There was a main effect of condition for both measures with injection videos showing increased physiological arousal than both accident videos and control videos. Error bars indicate $\pm 1SE$. * $p < 0.01$	105
B.1	The drift in each of the four conditions obtained on the entire sample. . . .	166
B.2	Differences in proprioceptive imprecision based on the preceding condition. . . .	168
B.3	The results collapsed across the two studies using RHI in vicarious pain responders. The final sample size was: controls, $N = 84$; S/L, $N = 41$; A/G, $N = 31$	169
C.1	Effect sizes for EC, EQ subscales, IRI subscales and HAS for S/L and A/G when compared to controls. Medium effect sizes (Cohen's $d > 0.5$) were observed on EC and EQ-ER for both S/L and A/G and on IRI-PT and IRI-F only for A/G. All the other effect sizes were small.	171

List of Tables

2.1	RHI questionnaire items and subscales.	30
2.2	Mean proprioceptive drift (mm) and standard deviations for each condition in each group.	33
3.1	Proprioceptive drift means \pm standard deviations in mm for each condition and in each group.	57
3.2	Medians for each condition and each subscale of the RHI questionnaire. . . .	61
3.3	Kruskall-Wallis H test results indicating differences between groups for each condition and subscale.	61

3.4	Means \pm standard deviations expressed in percentages of the difference between post-induction PSE and baseline PSE for each condition and in each group.	62
3.5	Medians in EI subjective ratings in each group and for each condition and subscale.	63
3.6	Kruskal-Wallis H test results indicating group differences in EI subjective ratings for each condition and each subscale.	63
4.1	Factor analysis results	82
5.1	Correlations between HR, HRV, Anxiety and Interoception	106
5.2	Summary of hierarchical regression analysis for variables predicting interoceptive accuracy ($*p < 0.05$; $**p < 0.01$)	107
5.3	Summary of hierarchical regression analysis for variables predicting heart rate variability (HRV) in the pain condition ($*p < 0.05$; $**p < 0.01$; $***p < 0.001$)	108
5.4	Summary of hierarchical regression analysis for variables predicting blood pressure in the pain condition	109
5.5	Summary of hierarchical regression analysis for variables predicting blood pressure in the pain condition	110
6.1	The initial aims and findings of each empirical chapter.	120
6.2	The findings for each group when compared to controls in each of the empirical studies conducted.	120
A.1	Number of subjects in each group for test and post-test generated with TPR or Intensity as cluster analysis variables.	162
A.2	Means and standard deviations for light subjective ratings according to the presence of light induced sensation.	163
A.3	Percentages of subjects experiencing the illusion in each group, namely participants who reported a positive proprioceptive drift	163
A.4	Percentages of subjects experiencing the illusion for each subscale of each condition, namely participants whose score was higher than 4	163
A.5	Percentages of subjects who scored higher than 4 for at least one of the subscales	164

B.1	RHI Questionnaire. Items and Subscales.	165
B.2	EI Questionnaire. Items and Subscales.	166
B.3	Correlation results between drift in each condition and questionnaire sub-scales.	168

Introduction

1.1 Vicarious pain perception

Some people experience the physical pain of others on their own body. As neurologist Joel Salinas confesses: ‘I distinctly recall one patient who in the setting of significant stress developed new self-mutilating tics. Watching him chew on the flesh of the right side of his face while grinding his teeth with all his force, I felt a painful buzzing run through the left side of my face and mouth that was so vivid that it bordered on hallucination. It was as if a stun gun was pressed against my face and triggered with each of his tics. The more forcefully he pushed, the more vivid the pain.’ (Salinas, 2017).

Mirroring the physical pain of others on one’s own body is an exceptional and intriguing ability identified only in a small proportion of the general population. So, why do these people feel the pain so intensely in their own body and how would this pain influence their behaviour or connection with the injured person or with other people? Some of these questions have been partially addressed, some are still waiting for an answer and this thesis will further investigate this phenomenon.

1.1.1 Vicarious pain perception: a general overview.

Vicarious pain perception represents the ability to experience the physical pain of others as one’s own (Giummarra and Bradshaw, 2008; De Vignemont and Jacob, 2012; De Vignemont, 2014). This phenomenon has been referred to as mirror-pain or synaesthesia for pain

since stimulation in the visual domain (i.e. seeing someone in physical pain) elicits a painful, somatic sensation in the observer (Fitzgibbon et al., 2010b).

The first anecdotal evidence of vicarious pain or synaesthesia for pain was documented in a patient with allodynia, a condition in which non-painful stimuli are perceived as painful, and, according to the patient's wife reports, he would feel pain when seeing her hurting herself but not when being told about an incident that she had suffered (Bradshaw and Mattingley, 2001). Interestingly, some of our participants classified as vicarious pain responders would report feeling localised pain when hearing about someone being in pain. For instance, participant AS reported feeling pain in her tooth when she was told the story of someone else suffering from a tooth infection. In line with these observations, the definition given by Giummarra and Bradshaw (2008) to pain synaesthesia was: 'the sensation in one part of the body (pain) produced by stimulus (pain) *observed* or *imagined* in another'. Synaesthesia for pain has been intensively documented in amputees who reported pain in their phantom limb or stump when seeing or thinking about someone else being in pain or when observing activities associated with pain (N.B. vicarious pain is different from phantom limb pain since it is always and exclusively triggered by somebody else's physical pain) (Giummarra et al., 2006), but also in women following traumatic childbirth (Giummarra and Bradshaw, 2008). Taken together, these cases seemed to indicate that vicarious pain was preceded by a traumatic painful experience or a chronic painful condition leading to heightened pain sensitisation. Particularly, the high incidence of synaesthesia for pain in amputees, present in approximately 16.2% of the cases, seemed to indicate that this phenomenon was somehow acquired (Fitzgibbon et al., 2010a; Goller et al., 2013). However, a study conducted by Osborn and Derbyshire (2010) recorded somatic responses to others' physical pain in the general population and about one third of their sample, whom they termed responders, reported vicarious pain. Their sample was relatively small; the authors screened 108 participants, 31 reporting a bodily feeling of pain when watching images of injured people. Moreover, their selection criteria were arbitrary. The authors used a mix of pictures and videos of injured people followed by a series of questions which asked participants to describe their experience and anyone who reported at least one pain experience was considered a pain responder. Subsequently, they invited a very small sample of 10 responders and 10 matched controls to take part in an imaging experiment where they observed significantly greater

activation in responders than in non-responders in both sensory and insular cortices, two brain regions associated with both emotional and sensory pain processing.

Grice-Jackson et al. (2017a) further characterized vicarious pain responders by dividing them into two groups based on the qualities of the somatic pain reported when witnessing pain. They followed a more systematic approach to identifying pain responders. Firstly, they screened a much larger sample (over 500 participants) and used a structured questionnaire (the Vicarious Pain Questionnaire (VPQ)). The VPQ presented videos of people suffering from accidents or having injections for greater authenticity of the experience and used a two-step cluster analysis on the questionnaire data to separate vicarious pain responders from non-responders. Importantly, they also distinguished between the quality of the pain felt, resulting in two clusters of responders: one sensory-localised and one affective-general one (for a more detailed explanation of the VPQ, see sections 1.1.2 and 2.3.2). Interestingly, the two groups summed up represented about 28% of the sample, a result similar to the one previously reported by Osborn and Derbyshire (2010). Nevertheless, the cluster analysis becomes more precise and conservative when the database is larger (Yim and Ramdeen, 2015) and the research conducted as part of this thesis addresses this issue by running the analysis on a much larger sample size (1000+) and by conducting a test-retest reliability analysis of the questionnaire (see section 2.4.1).

In the next sections, the theories and mechanisms of vicarious pain will be further explored. This phenomenon will be referred to as vicarious pain perception and the individuals manifesting it as vicarious pain responders. This is because the term synaesthesia for pain has not been consistently used and because it is still under debate if mirror sensations are truly synesthetic. On one hand, these phenomenon fits well the definition of synaesthetic experiences, namely that stimulation in one sensory domain (i.e. sensory-visual) elicits an involuntarily response in a different domain (i.e. sensory-somatic) (Ward and Banissy, 2015). On the other hand, there are a series of differences between other synesthetic conditions (e.g. grapheme-colour synaesthesia) and mirrored pain or touch sensations. These include the lack of idiosyncrasy in mirrored-sensory responses (the pain felt by individuals with mirror touch or pain has similar characteristics), the higher incidence in these populations (over 20% compared to 1-2%), and its dependency on the social context which makes them more similar to socially contagious

phenomena such as laughter (Provine, 1992), yawning (Provine, 1989; Platek et al., 2004), and itching (Ward et al., 2013) (for a more detailed account see Rothen and Meier (2013)).

1.1.2 Vicarious pain questionnaire and qualities of vicarious pain.

Different bodily reactions may be triggered when witnessing the physical pain of others (Giummarra et al., 2015). As such, two main qualities of vicarious pain have been distinguished: sensorial and affective. Grice-Jackson et al. (2017a) developed the Vicarious Pain Questionnaire (VPQ), a measure tailored to differentiate between sensorial and affective qualities of vicarious pain. This measure presents participants with 16 10s-long videos which depict people experiencing physical pain such as accidents or injuries and questions the observer about any bodily felt pain sensations including pain intensity, localisation and other qualitative attributes. The bodily localisation of the pain may be localised to a certain body part the same or a different one or generalised to the entire body. The bodily pain felt may be described using sensorial adjectives such as ‘tingling’, ‘burning’, ‘stinging’ or affective adjectives such as ‘nauseating’, ‘gruelling’, ‘aversive’. Using a two-step cluster analysis on the recorded answers, three distinct groups are identified: 1) non-responders or controls (who report no pain when watching a video with someone else experiencing physical pain), 2) sensory-localised responders (S/L) (who report a localised feeling of pain at the same location as the person in the video and tend to use sensory descriptors) and 3) affective-general responders (A/G) (who report a generalised and emotional feeling of pain).

The questionnaire has been used since its development to identify the three groups and significant structural and functional brain differences prove their validity. Structural brain analyses indicated increased grey matter density in the insular and somatosensory cortices and decreased grey matter density in the right temporoparietal junction (rTPJ) in both groups of vicarious pain responders when compared to controls (Grice-Jackson et al., 2017a). Functional analyses indicated enhanced coupling between the rTPJ and the bilateral insula (Grice-Jackson et al., 2017b). This study employed a restrictive sample size, but greater than the one in Osborn and Derbyshire (2010) study (14 A/G, 18 S/L, 30 controls, compared to 10 responders and 10 non-responders), the results obtained being



Figure 1.1: An example of an accident video presented in the VPQ and a series of questions assessing various qualities of pain such as intensity and localisation.

comparable to the previous study.

This thesis will employ the VPQ and it will further address its reliability by conducting test-retest analyses and explore the differences and characteristics of the two groups of vicarious pain responders previously identified and characterised by [Grice-Jackson et al. \(2017a\)](#). Its focus will be on bodily-self representations in these groups in relation to others.

1.2 Theories of vicarious pain perception.

1.2.1 Core trauma and chronic pain as precursors for vicarious pain.

[Fitzgibbon et al. \(2010b\)](#) propose that vicarious pain perception develops following painful events and/or medical conditions such as traumatic injuries or chronic pain. According to the authors, exposure to traumatic injuries or chronic pain may lead to an atypical processing of physical pain due to: a) central sensitization of spinal cord fibres resulting in neuropathic pain; b) hypervigilance to pain cues; c) disinhibition of mirror system for pain.

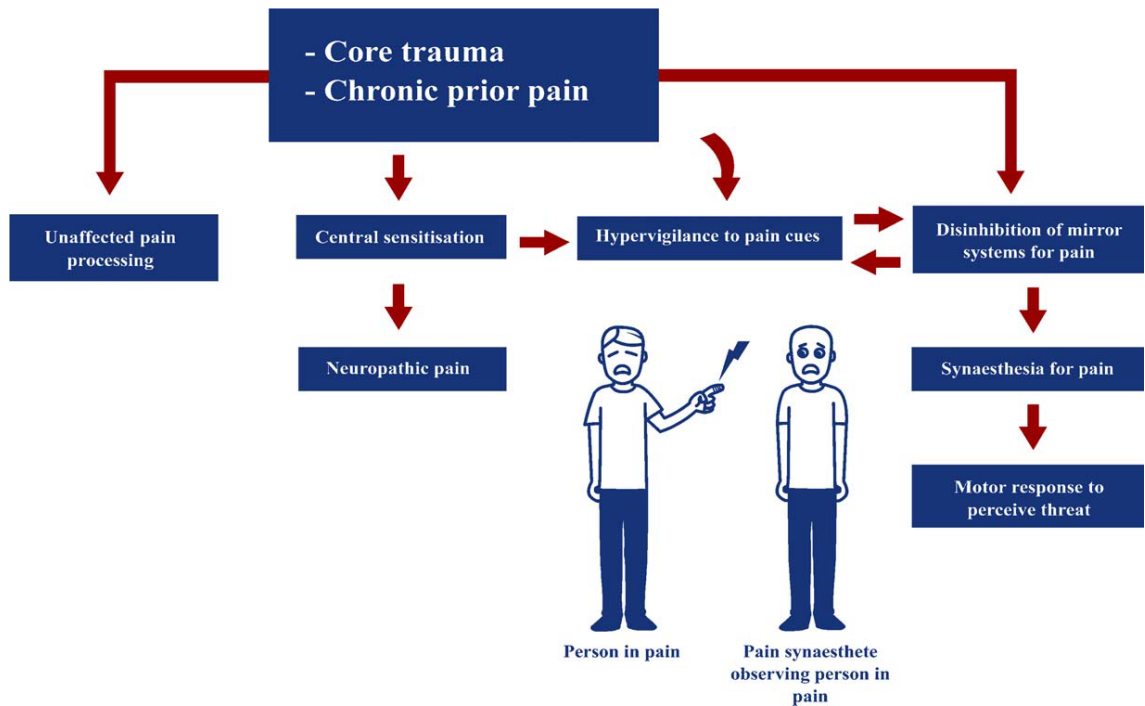


Figure 1.2: A schematic representation of Fitzgibbon and colleagues model of vicarious pain. Taken from [Fitzgibbon et al. \(2010b\)](#).

Within the model's framework, central sensitisation occurs as an adaptive mechanism following exposure to intense pain experiences, leading to lower pain thresholds and to enhanced focus on potentially threatening stimuli ([Rollman et al., 2004](#)). Additionally, it can be influenced by cognitive, emotional, and attentional processes such as hypervigilance to pain cues ([Zusman, 2002](#)). Attention to painful cues can also modulate perceived intensity of pain and neuronal activity in brain pain matrix regions ([Mu et al., 2008](#); [Gu and Han, 2007](#)). For instance, participants rated pictures depicting pain as more painful when asked to attend to the pain rather than distracting elements such as number of hands in the pictures and higher activity in response to them was recorded in the ACC and paracingulate cortex. Moreover, ACC response activity was also modulated by stimuli' veracity, being increased in response to pictures depicting real hands rather than cartoons ([Gu and Han, 2007](#)).

All these different processes may interact and result in the acquired experience of vicarious pain. The disinhibition of the mirror system would occur as a consequence of central sensitisation to pain and to the selective attention towards pain cues and it would primarily facilitate the vicarious pain experience by overcoming the given threshold for pain awareness. This disinhibition would manifest in areas of the pain matrix including

the thalamus, anterior and posterior insula, anterior cingulate cortex, premotor cortex, supplementary motor area, and somatosensory cortices (for a meta-analysis, see [Lamm et al. \(2011\)](#)). Importantly, seeing someone else in pain activates neural circuitry involved in the physical perception of pain ([Singer et al., 2004](#); [Jackson et al., 2006](#)). Thus, vicarious pain would correspond to a heightened sensitivity in brain's pain matrix responding to both self and other's pain.

Interestingly, the specificity of the pain matrix has been recently questioned. Various studies have indicated that non-nociceptive stimuli can elicit responses in the pain matrix and that the correlation between pain intensity and the magnitude of the neuronal response can be disrupted ([Mouraux and Iannetti, 2009](#); [Iannetti et al., 2008](#); [Treede, 2003](#)). [Mouraux et al. \(2011\)](#) identified multimodal responses in the "pain matrix" to salient non-nociceptive stimuli. The magnitude of multimodal responses correlated significantly with the perceived saliency of the stimulus and it was determined by stimulus' task relevance, indicating an interplay between bottom-up and top-down cognitive processes. The various types of stimuli (i.e. nociceptive, somatosensory, auditory, and visual) triggered haemodynamic responses in the insula, S2, and ACC indicating that these regions, particularly the ACC, are involved in evaluating a stimulus and the opportune action in response to it, regardless of its nociceptive nature ([Mouraux et al., 2011](#); [Iannetti and Mouraux, 2010](#)). Other studies have shown that the magnitude of ERPs in response to painful stimuli did not correlate with the pain intensity elicited by a second or a third stimulus delivered at a constant inter-stimulus interval. This suggests that, in the absence of the 'surprise element' of a first stimulus, there is a reduction in the neuronal response in the "pain matrix" most likely related to the fact that the repeated stimulus is both less novel and less unpredictable ([Iannetti et al., 2008](#)). Therefore, the activation of the pain matrix seems to be triggered by the saliency of a stimulus which is defined by how much the stimulus contrasts with its surroundings rather than its sensorial qualities ([Fecteau and Munoz, 2006](#); [Knudsen, 2007](#)). The saliency hypothesis provides a model which can explain various findings in the empathy for pain research such as the "pain" responses to watching a noxious stimulus delivered to another individual or watching a cue indicating the delivery of such a stimulus (in particular to someone we care about ([Singer et al., 2004](#); [Jackson et al., 2006](#)), to watching a menacing stimulus such as a needle approaching the hand ([Cheng et al., 2007](#)), or experiencing

social rejection (Eisenberger et al., 2003). These stimuli do not activate nociceptors but have a high saliency content. Regarding vicarious pain responses, the increased activity in regions associated with the pain matrix (e.g. somatosensory and insular cortices) may denote either a higher sensitivity to real or imagined pain or a higher attention to salient cues (pain specific or not). Further research which is beyond the scope of this thesis is needed to elucidate these claims.

In brief, this model proposes that pain experiences cause disinhibition of mirror activity encountered in the pain matrix, resulting in vicarious pain experiences. The model emulates well on the numerous documented cases of vicarious pain responders in amputees (Giummarra et al., 2006), after traumatic labour (Giummarra and Bradshaw, 2008), including on findings showing more intensive vicarious pain activity in the pain matrix in chronic backpain patients (Vachon-Presseau et al., 2013). Nevertheless, it presents vicarious pain as an acquired disturbance. As such, it is not sufficient since it cannot account for the entire picture, namely that vicarious pain responses have been recorded in the general population in the absence of previous pain traumatic incidents and that not all people that experience traumatic incidents develop vicarious pain.

Notably, the core of this theory, namely the disinhibition or, in other words, over-excitability of the mirror neuron system overlapping the pain matrix system, has been proposed as a central mechanism by others schools of thought which extended it to more general mirroring mechanisms related to the sensorial and phenomenological bodily self (see De Vignemont (2013) for an overview).

1.2.2 Enhanced mirroring activity in vicarious pain perception.

Mirror neurons were first discovered in studies performing single-cell recordings in the F5 area of the ventral premotor cortex in macaque monkeys (Rizzolatti et al., 1988). It was observed that these neurons fired when the macaque performed a specific action but also when it observed the action being performed by another macaque or the experimenter. Subsequently, mirror neurons were identified in humans, fMRI studies revealing activations in brain regions such as Broca's area and premotor cortex when actions were performed by the participants or simply observed (Buccino et al., 2004). These findings evidenced the existence of a mirror neuron system (MNS) displaying matching brain

activity in the action execution and observation and localised to premotor and inferior parietal cortices (Molenberghs et al., 2016). Importantly, mirror-motor activity has been recorded at a neuronal level but also muscular level suggesting that it can influence motor behaviour (Fadiga et al., 2005) and that it can have implications for mimicry and action-understanding. This activity reaches only subthreshold levels, but it is sufficient to influence behavioural responses. For example, in an imitation-inhibition task, participant's reaction times are significantly influenced by the match or mismatch between the finger movement they are instructed to perform and finger movement that they observe on the screen. If the movement of the finger that they observe is incongruent to the one that they are asked to perform (i.e. seeing the right index finger being lifted and instructed to lift the right middle finger) their reactions times are larger (Brass et al., 2001). Another example is represented by facial mimicry where capturing the other's emotional state is mediated by the accuracy of facial imitation (Braadbaart et al., 2014). Thus, MNS is believed to be involved in covertly imitating other's goal-directed actions which would lead to their better understanding and to empathic responses in the observer (Buccino et al., 2004; Rizzolatti et al., 2002; Fadiga et al., 2005).

The mirror motor activity was the first to be discovered but subsequent research indicated that mirroring processes are not confined exclusively to actions. Mirroring neuronal activity was recorded in response to observed touch (Keysers et al., 2004) and pain (Jackson et al., 2006) in another individual providing supporting evidence for the presence of shared cortical networks for vicarious sensations. For instance, the same neuronal pain matrix including both sensory and motor regions of the cortex becomes active when seeing that someone else is in pain or when the pain is self-inflicted (Jackson et al., 2005). The activation recorded in cortical networks in response to sensorial or motor observations would constitute the substrate for shared emotional states between self and others rooted in bodily and neuronal responses (Gallese, 2003). As such, vicarious pain sensations have been linked to shared self-other representations and empathetic responses (Singer et al., 2009). Moreover, according to certain accounts, these shared representations imply a correspondence between body parts and neuronal networks facilitating the mapping of the other's physical states onto one's own and leading to a greater understanding of the other (Gallese and Goldman, 1998). This approach aligns with theories of embodied cognition (Niedenthal et al., 2005) sustaining that cognitive

representations are rooted in bodily states and neuronal mirroring systems.

A more detailed account of the shared self-other representations in vicarious pain perception from both a bodily and affective perspective will be given in section 3 which will also constitute the focus of this thesis.

1.2.3 Mirroring activity and activation of simulation mechanisms in vicarious pain perception.

Sensory and motor neuronal activation analogous to mirror neuron activation occurs when someone imagines the sensorial experience of another (Gallese, 2003). Decety and Grèzes (2006) underline the importance of simulation for social functioning since the individual does not rely purely on the environmental cues and the proximal reality but generates internal representations of the world and others' states. Thus, simulating the physical pain of another person may result in a spectrum of sensations translated in the great variability of the quality of the pain described based in interindividual differences and prior experiences. Interestingly, this simulation may occur at an overt level when the individual is aware of his/her intention to simulate and has a specific aim (pragmatic simulation) or at a covert level when it happens spontaneously, and the individual is not aware of his/her intention to simulate (Decety and Grèzes, 2006). The spontaneity of the experience seems to be crucial for vicarious pain perception since there is no report of active simulation of the pain observed. For instance, when climbers are asked to imagine a difficult climbing route, they recall the route and activate a motor, embodied simulation of that memory more than novices (Pezzulo et al., 2010). This process occurs spontaneously and depends on prior experiences, its manifestation being stronger if preceded by training or great exposure to the specific stimuli. Analogously, both imagined and observed sensory experiences correlate with somatosensory activation (Schmidt et al., 2014; Ebisch et al., 2008) and pain induced through suggestion presents similar patterns of activation as physically felt pain (Derbyshire et al., 2009; Patterson and Jensen, 2003).

Extrapolating to our sub-group of the population, it has already been shown that mirror pain responders display greater somatosensory activation when witnessing someone else in pain (Grice-Jackson et al., 2017a) and, possibly, they would display it when asked to recall or imagine oneself or others being subject to painful sensory stimuli. These

speculations are also in line with the first theory emphasising the importance of prior exposure to trauma and chronic pain in VPP and directly linked to the ‘mirroring activity’ with the mention that it emphasises the act of imagining rather than simply observing.

In conclusion, the exact mechanisms of vicarious pain perception are far from being understood. The interpretations of this phenomenon vary covering proposals such as sensitization to pain following an accident or chronic condition, disinhibition of mirror neurons, and increased imaginative and simulation abilities. These various theories seem to complement each other and are likely to be interlinked. Regardless of the exact cause, the manifestations of vicarious pain seem to be inherently related to bodily self and other mechanisms. This thesis will focus on understanding the link between vicarious pain perception and self-other representations and differentiation from both a bodily and an affective point of view.

1.3 Shared self-other representations in vicarious pain responders: the link with empathy.

The ability to mirror the physical pain of others has been attributed to shared self-other representations manifested as corresponding automatic and somatic responses in the observer (Preston and De Waal, 2002) and underpinned by co-activation in neuronal networks underlying embodied phenomena such as the somatosensory and insular cortices (Keysers et al., 2004; Singer et al., 2004). This ability (to co-represent the others’ feelings) has been linked to empathy (De Vignemont and Singer, 2006; Lockwood, 2016) which was considered to rely primarily on mirroring activity of both sensory and motor manifestations (Rizzolatti et al., 2002; Fadiga et al., 2005). Thus, the identification with the other’s state has been regarded as fundamental for empathetic responses defined as the capacity to share and understand the emotional states of the others (Gallese, 2003). However, theoreticians have drawn attention upon the fact that the transition between feeling and understanding the other’s state is not self-explanatory and does not occur spontaneously. Sharing the immediate feeling of the other’s state also called emotional contagion is considered a precursor of empathy but not a sufficient condition for it to occur (Bird and Viding, 2014). Bernhardt and Singer (2012) refer to three main aspects

of empathy: affective empathy (i.e. emotional contagion), cognitive empathy theory of mind (ToM) or perspective taking and compassion, the action to alleviate other's suffering. As such, the affective aspect of empathy is a crucial process which allows recognising and simulating others' emotional states, but it does not necessarily require a cognitive understanding of these states. A widely accepted model states that empathy for pain involves coactivations in networks outside of the pain matrix and other than affective and/or sensory including regions associated with self-other regulation. These networks are mainly associated with perspective taking in terms of both self-other orientation and bodily location and networks associated with social cognition extracting the salient information available in the environment (Bird and Viding, 2014; Decety, 2011).

In their model of empathy, Bird and Viding (2014) address the importance of self-other regulation and propose a more sophisticated mechanism in which the distinction between self and other is constantly maintained. According to the authors, 'for empathy to have occurred, the requirements for emotional contagion have to be met, and in addition the perceiver has to explicitly 'tag' their affective state as being experienced by the other.' (Bird and Viding (2014), p.521). They emphasise the crucial role of self-other switch responsible for self-other regulation and constantly changing perspective from self to other and vice-versa. The default state of the self-other switch is the self so, in specific social situations, the switch engages in an active process that suppresses self-perspective and enhances the other perspective. The self-other switch relies on the interplay between two systems: a) the Theory of Mind system which represents the ability to understand the mental states of others and its main neuronal substrates are represented by the temporoparietal junction, medial prefrontal cortex and precuneus (Frith and Frith, 2006) and b) the Affective Representation System which encodes the current affective state of the self and its main neuronal substrates are the insular and anterior cingulate cortex (Craig, 2002; Critchley et al., 2004). Thus, this control mechanism actively modulates the focus of attention towards other people whilst suppressing the self-focus or sustains the focus of attention on the self in the detriment of others. Further evidence has indicated that balanced self-other representations play a crucial role in the processing of other's emotional states and social interactions. For instance, training the ability to regulate self-other representations in the motor domain has been linked

to more pronounced physiological and subjective responses to observation of pain in others (de Guzman et al., 2016).

The principal brain region acting as a switch between the self and others is considered to be the right temporoparietal junction (rTPJ) (Bird and Viding, 2014). There is a fair amount of evidence supporting the involvement of this region in various psychological tasks which need attention to be switched between self and other including the egocentric bias (Silani et al., 2013), perspective taking (Mazzarella et al., 2013), motor imitation-inhibition (Santiesteban et al., 2015), bodily ownership and location (Tsakiris et al., 2008). In our samples of vicarious pain responders, structural and functional differences have been identified in regions other than the ones responsible for somatosensory mirroring which included the rTPJ (Grice-Jackson et al., 2017a). Considering the sensory and neuronal particularities of vicarious pain responders as well as their ability to literally feel what the other feels within the self-other regulation model, it may be speculated that vicarious pain responders have a tendency to actively inhibit the self and enhance the other.

A similar speculation has been formulated in a subgroup of the population characterised by vicarious tactile responses, namely Mirror Touch Synaesthetes (MTS). The Self-Other Theory (Ward and Banissy, 2015) has been formulated based on findings indicating differences in parietal (i.e. decreased grey matter density in rTPJ) and prefrontal regions (i.e. reduced grey matter in mPFC) (Holle et al., 2013) which have been mainly associated with perspective taking and Theory-of-Mind (ToM) processes (Frith and Frith, 2006). The Self-Other Theory refers to impairments in the ability to distinguish and control between self and other and evidence has shown that MTS have difficulties in inhibiting the other and enhancing the self but not vice-versa (Santiesteban et al., 2015). These particularities may be manifested in the socio-cognitive domain, in the control of self and other actions or experiences, and in bodily self-other representations. However, this overlap cannot be complete since this would pose serious problems to normal functioning (Bird and Viding, 2014). Notably, MTS and sensory-localised vicarious pain responders tend to co-occur, albeit with MTS being rarer (Ward et al., 2018), and some people have collectively referred to them as mirror-sensory synaesthesia (Ward and Banissy, 2015).

Altogether, there is a fair amount of evidence showing that particularities in shared

self-other representations are linked to vicarious tactile perceptions and that this system plays an important role in vicarious pain perception. Particularities in the self-other system may tap into differences in both bodily self-other representations as well as affective and cognitive shared representations which will be separately discussed in the next sections and constitute the focus of this thesis.

1.3.1 Shared bodily representations in vicarious pain perception.

The existence of mirroring mechanisms for both sensorial experiences and motor actions paved the way towards defining shared bodily dimensions between self and other. Furthermore, it has been suggested that knowledge about one's own body would be used to decode the other's perception and actions and that correspondence between body parts as well as cortical regions of activity would be an immutable condition for vicarious experiences as if the observer would map the subject onto one's self (Goldenberg and Karnath, 2006). Findings of studies looking at vicarious responses to pain seem to support this proposal. For instance, muscle-specific inhibited motor-evoked potentials were recorded when a participant observed someone else's hand or foot being penetrated by a needle. These responses occurred in the muscle that corresponded to the one being penetrated and were modulated by sensory but not affective qualities of pain (Avenanti et al., 2005). Moreover, observation of pain in others induces motor responses which are influenced by congruency of body parts as well as a generalised body excitability response (Avenanti et al., 2009). Regarding cortical mapping of pain, somatosensory-evoked potentials are selectively modulated by pain intensity indicating that pain responses are encoded onto the somatotopically organised region of the primary somatosensory cortex which extracts sensorial features of pain such as localisation and intensity (Bufalari et al., 2007). This evidence suggests that shared representations between self and other are encoded in bodily terms and that vicarious pain is embodied. This is in agreement with the idea that pain is inexorably linked to the spatial structure of the body and its mapping affects body movements and posture. The brain networks where physical pain is processed including somatosensory, insular, and parietal projections provide specially organised tactile representations and encode bodily tactile locations providing the substrate for special orientated responses to pain (Haggard et al., 2013).

Vicarious pain is mapped on the observer's body influencing its representation, but, at the same time this mirror sensory experience of another person on one's own body may reflect an over-inclusive body ownership mechanism and a greater tendency to treat all observed bodies as self-related or as a top-down orienting mechanism for selective attention to the self that inhibits representations of the (non-self) other (Bird and Viding, 2014; Tsakiris et al., 2008; Northoff et al., 2011). Therefore, vicarious pain responders may incorporate others' experiences into their own body representations modelling physical boundaries between self and other.

Bodily ownership: the rubber hand illusion and enfacement illusion paradigms.

The intersubjective correspondence between both physiological and neuronal responses to pain previously described poses problems to the distinction between bodily self and other representations. Intrinsic overlaps between bodily perceptions and actions would impair the ability to develop a strong sense of self bodily identity and ownership. As De Vignemont (2013) poses the question: 'If at some level the representation of one's body is similar to the representation of other people's bodies, then how could it ground the sense of ownership?'.

One way to test this would be by measuring bodily ownership in these groups and their propensity to incorporate or to extend ownership over other bodies. The sense of body ownership arises from integration and correlation of intermodal sensory signals which contribute to the shape of a coherent bodily self separated from the outer world or other similar objects (Botvinick and Cohen, 1998; Ehrsson et al., 2004). Various paradigms have been employed to manipulate bodily ownership and to underline how correlation of incoming intermodal signals contribute to the sense of bodily self. The rubber hand illusion (RHI) is the most popular paradigm used to study body ownership (Botvinick and Cohen, 1998). A second paradigm which has been widely used is the enfacement illusion (EI) (Tsakiris, 2008; Sforza et al., 2010). They will both be used in articles I and II of this thesis and represent the main paradigms to study bodily ownership in vicarious pain responders.

In the RHI, participants tend to report that they feel ownership over a dummy hand

thus expanding their own bodily boundaries. The paradigm consists of placing a dummy hand in front of the participants whilst their real hand is hidden from view. Subsequently, both hands are stroked either synchronously (at the same time) or asynchronously (out of phase) and most evidence shows that the illusion is stronger in the synchronous condition (Botvinick and Cohen, 1998; Tsakiris and Haggard, 2005).

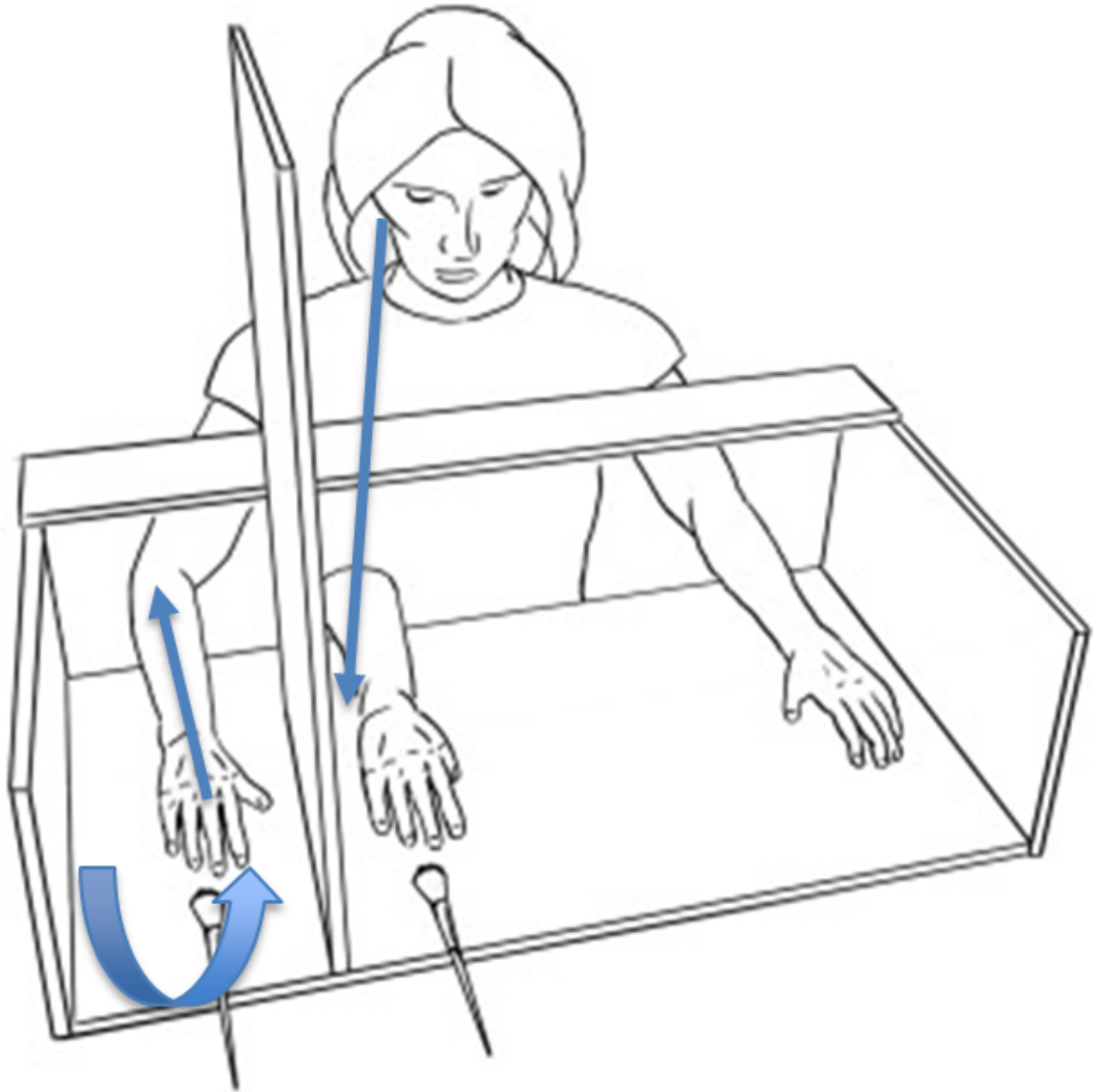


Figure 1.3: A schematic representation of the RHI paradigm indicating the incoming sensory signals including vision, touch and proprioception.

The main theoretical accounts of this paradigm propose that the RHI arises mainly from the integration of proprioceptive, visual and somatosensory inputs which are processed according to the internal body representation, the illusion being stronger when the external inputs match each other but also the internal representation of the body (e.g. the hand has the same orientation, colour or is within the peripersonal space) (Costantini

and Haggard, 2007). Furthermore, cognitive accounts of the RHI emphasise a central role of top-down processes which influence the experience since expectancies and trait differences impact objective and subjective results obtained following induction suggesting that performance of this task cannot be attributed to multisensory integration alone (Alsmith, 2015; Haans et al., 2012).

A Bayesian framework has also been formulated considering multisensory integration by taking into account the weight of incoming signals (bottom-up processes) and predictions or expectations concerning these signals (top-down processes). The Bayesian sensory model uses causal inference to predict optimal estimates of location and time which are subsequently matched to the actual incoming sensory signals (Samad et al., 2015). Thus, a match between expectations and input signals would result in a greater likelihood of experiencing the illusion, as it usually happens in the synchronous condition but not in the asynchronous condition when there is a temporal delay. Moreover, within this framework, more precise signals weigh more and overwrite less precise ones. As such, baseline confusion in the incoming sensory signals would generate an experience in accordance with and heavily influenced by prior expectancies.

The enfacement illusion (EI) is a facial analogue of the RHI, which uses tactile facial stimulation to manipulate the perceived similarity with ‘the other’. During the EI, touch is delivered to the participants’ face whilst they watch an induction video presenting mirrored touch delivered to an unfamiliar model’s face (Tsakiris, 2008; Sforza et al., 2010). The touch is delivered synchronously or asynchronously and before and after each induction video measures of perceived similarity between the participant and the model are taken by asking participants to judge if the morphed faces that they see look more like themselves or like the other. Synchronous touch generates an increase in perceived similarity and feelings of ownership and agency over the model’s face (Tajadura-Jimenez et al., 2011). Similarly, to the RHI, EI further exploits integration of multisensory signals such as vision and touch to update the internal mental representation of self based on prior expectations (Tsakiris, 2008).

The studies conducted in articles I and II of this thesis employed the RHI and EI as the main paradigms in order to better understand the malleability of body ownership in vicarious pain responders in light of the various existing theories explaining this phenomenon. Our main hypothesis and expectation was that vicarious pain responders



Figure 1.4: The set-up of the Enfacement Illusion paradigm. The image was taken from [Tajadura-Jimenez et al. \(2011\)](#)

would have a greater tendency to treat other bodies as their own and thus, they would show a greater propensity to incorporate ‘the other’ as measured by performance on these two paradigms. Previous research indicated that there is a greater tendency in vicarious pain responders to incorporate the rubber hand ([Derbyshire et al., 2013](#)) and evidence from studies conducted on MTS showed that they tend to report greater ownership over both a dummy hand and a model’s face ([Davies and White, 2013](#); [Maister et al., 2013](#)). However, this research did not distinguish between the qualities of the pain felt and did not investigate further the significance of the results within bodily ownership theories. As such, articles I and II will address these gaps.

1.3.2 Shared affective representations in vicarious pain responders.

Vicarious pain responses have a strong affective component: the immediate and intense sharing of the painful state of the other, a contagious sensory and emotional response to the other’s pain. As intuitive as this may seem, a few questions still arise: a) Is this ‘contagious pain’ a subset of a more general form of emotional contagion?; b) Does sharing the emotional states of the other impact the cognitive appraisal of those states? Does it influence others’ representations and the relations with them?; c) Can this ‘painful

contagion' cause personal distress?

It has already been established that vicarious pain responders activate sensory-motor processes through mimicry mechanisms in a more pronounced way than the rest of the population and there is a fair amount of evidence supporting this view with various studies finding increased grey matter density and cortical activity in regions such as the somatosensory cortex (Grice-Jackson et al., 2017b; Holle et al., 2013; Blakemore et al., 2005). Their propensity to co-represent the others' emotional states may be linked to their atypical ability to distinguish between self and other which, as previously stated, influences both the socio-cognitive domain of perspective taking and mentalizing processes as well as bodily self-other representations (Bird and Viding, 2014; Frith and Frith, 2006). Brief evidence coming from behavioural studies indicates that vicarious pain responders may display differences in perspective taking and that they are more influenced by the visual perspective of an avatar when judging from their own viewpoint, being quicker in taking the other's perspective in consistent trials (but the authors did not differentiate between different kinds of responders) (Derbyshire et al., 2013). However, there are opposing views on whether feeling the physical pain of another benefits or impairs social interactions. On one hand, emotional contagion can lead to empathic concern and altruistic behavior (Batson et al., 1981, 1997), on the other hand, it can lead to higher personal distress and avoidant behavior (Bloom, 2017). Some evidence indicates that pain sensitivity correlates with pain anxiety and anxious traits (Palit et al., 2015) and that anxiety is an important co-variate in regulation of emotional responses in vicarious pain responders (Nazarewicz et al., 2015), but there is also evidence suggesting that heightened responses to the pain of others are associated to empathic behaviours (Jackson et al., 2005; Hein et al., 2011). Furthermore, one more variable could mediate these behaviours: emotion regulation which represents the ability to respond to emotional stimuli in an adaptive manner (Gross, 1998). Studies have shown that emotion regulation is linked to better cardiac autonomic regulation which can be improved in response to pain exposure (Appelhans and Luecken, 2008; Meeus et al., 2013; Riganello et al., 2019; Tracy et al., 2018). The extent to which vicarious pain is related to emotional contagion and emotional self-regulatory abilities is not known and it will be addressed by this thesis. It will also be investigated how vicarious pain processing can influence social closeness and self-other associations. Another important aspect of vicarious pain

responses is that they are based in mirroring responses which can be manifested at a somatic and physiological level (Preston and De Waal, 2002). As such, vicarious pain responses have been linked to autonomic changes similar to the ones experienced in one-self (Levenson and Ruef, 1992). The most prominent physiological changes are represented by arousal and an increase in measures such as heart rate, blood pressure and skin conductance (Garfinkel et al., 2015b; Fernández et al., 2012). Physiological responses in vicarious pain responders will thus be investigated as part of this thesis together with other social and emotional processes in articles III and IV.

1.4 Aims

Vicarious pain experiences are present in a considerable percentage of the population and they have been of great interest in the scientific community. Various theories have emerged in recent years and evidence has mostly linked them to mirroring and/or simulation mechanisms but, the processes underlying these manifestations and their place within a wider phenomenological dimension are not completely understood. They have been mainly attributed to particularities in empathic traits, self-other differentiation and imaginative abilities thus, this unique condition has the potential to contribute to psychological and social developments. Through a combination of behavioural, physiological and questionnaire studies, this thesis aims at developing a better scientific understanding of vicarious pain experiences in general and their links to more specific processes including bodily ownership and intersubjective experiences. The main aims of this thesis which will be addressed in the empirical chapters are:

- 1 To investigate bodily ownership in vicarious pain responders (Article I)
- 2 To explain particularities in bodily ownership of vicarious pain responders within current theories of multisensory integration, namely the Bayesian Sensory Inference model (Article II).
- 3 To investigate the influence of vicarious pain perception on empathic traits and self-other associations (Article III)

-
- 4 To explore physiological reactivity in these subgroups and possible coping mechanisms that would contribute to the normal functioning of these individuals (Article IV).

Article I: Atypical Susceptibility to the Rubber Hand Illusion linked to Sensory-Localised Vicarious Pain Perception

2.1 Abstract

The Rubber Hand Illusion (RHI) paradigm has been widely used to investigate the sense of body ownership. People who report experiencing the pain of others are hypothesised to have differences in computing body ownership and, hence, we predicted that they would perform atypically on the RHI. The Vicarious Pain Questionnaire (VPQ), was used to divide participants into three groups: (1) non-responders (people who report no pain when seeing someone else experiencing physical pain), (2) sensory-localised responders (report sensory qualities and a localised feeling of pain) and (3) affective-general responders (report a generalised and emotional feeling of pain). The sensory-localised group, showed susceptibility to the RHI (increased proprioceptive drift) irrespective of whether stimulation was synchronous or asynchronous, whereas the other groups only showed the RHI in the synchronous condition. This is not a general bias to always incorporate the dummy hand as we did not find increased susceptibility in other conditions (seeing touch without feeling touch, or feeling touch without seeing touch), but there was a trend for this group to incorporate the dummy hand when it was stroked with a laser light. Although individual differences in the RHI have been noted previously, this particular pattern is rare. It suggests a greater malleability

(i.e. insensitivity to asynchrony) in the conditions in which other bodies influence own-body judgments.

2.2 Introduction

The rubber hand illusion (RHI) paradigm (Botvinick and Cohen, 1998) is an established means of investigating and manipulating the sense of body-ownership including body location, image, and agency (Ehrsson et al., 2004; Tsakiris and Haggard, 2005; Longo et al., 2008). In this paradigm, the participant's hand is hidden from view and a dummy hand is placed in view, alongside the real hand. The hidden and dummy hands are then stroked either synchronously or asynchronously. The illusion is significantly stronger in the synchronous condition, when the participant feels the touch delivered to the visible dummy hand as if the hand belonged to him/her. Thus, when the illusion occurs, the rubber hand becomes temporarily incorporated in the participant's mental body representation. This is reflected in a perceived shift in the position of one's own hand towards the fake hand, a phenomenon termed proprioceptive drift. The objective measure of proprioceptive drift complements self-reported questionnaire ratings through which participants report their experience of ownership, self-location, and agency over the fake hand.

The RHI arises through the integration of multisensory information with reference to a prior mental body representation (Costantini and Haggard, 2007). According to this model, visual, proprioceptive, and somatosensory inputs are processed within higher order multimodal integration areas (Ehrsson et al., 2004; Limanowski and Blankenburg, 2015). As such, the illusion is the strongest when distinct external inputs match each other (as shown by the difference between synchronous and asynchronous stroking, (Botvinick and Cohen, 1998)) and also when external inputs match internal representations of the body (Tsakiris, 2010).

The RHI is greater when the rubber hand looks similar, has same orientation and side as the real hand (e.g. both left or both right) and when the hand is within the peripersonal space (PPS) of the person (Preston, 2013). Thus, the viewed object is tested against an abstract model of one's body for 'fit', to determine whether or not the dummy hand is incorporated within the body model in a process that involves both bottom-up and top-down mechanisms (Tsakiris et al., 2008). In some circumstances, the illusion can also occur in the absence of visuo-tactile congruency. The illusion can be induced in a 'light only' condition, when the dummy hand is 'stroked' by a laser-pointer but no light/tactile

stimulation is applied to the real hand (Durgin et al., 2007). Here, participants who report tactile and thermal sensations evoked by the light-beam also report stronger feeling of ownership of the dummy hand.

Atypical performance on the RHI has been linked to various psychiatric and developmental conditions, as well as sub-clinical individual differences. Differences in the RHI are observed in patients with autism (Paton et al., 2012; Palmer et al., 2013), schizophrenia (Thakkar et al., 2011), neurotypical variations linked to schizotypy (Germine et al., 2013; Kállai et al., 2015), in eating disorders including anorexia nervosa (Eshkevari et al., 2012; Kaplan et al., 2014), and in mirror-touch synaesthesia (Davies and White, 2013). In the latter, participants report experiencing touch when seeing others touched and, during the RHI paradigm, report ownership of the rubber hand when it is stroked but no physical touch is applied to the participant's own hand. This may occur because the observed touch triggers a synchronised feeling of touch on their own body, analogous to the normal effect of synchrony in the RHI (Davies and White, 2013). However, it may also reflect more general differences in computing body ownership in this group: in effect, a tendency to misattribute other people's bodies as their own (Ward and Banissy, 2015). In the present study, we extend this to a similar related phenomenon, mirror-pain synaesthesia, namely to individuals who report feeling pain when seeing pain in others.

Various manipulations of the illusion have been previously used altering the perfect congruency of the illusion corresponding to the synchronous condition. These have included seeing touch without physically feeling it (Davies and White, 2013), projecting a laser beam on the dummy hand (Durgin et al., 2007), or simply looking at the dummy hand without any other stimulation (Rohde et al., 2011; Samad et al., 2015). Manipulations of the quality of the material used to stroke the rubber hand or the anatomical position of the real and rubber hands have also been employed. The stimulation has been conducted using soft or rough fabric (Schütz-Bosbach et al., 2009; Filippetti et al., 2019) thus manipulating the congruency of the quality of the sensorial feeling rather than the temporal congruency of stimuli delivery and indicating that the experience of the RHI is stronger in a congruent condition. The position of the rubber hand has been used in anatomically plausible or implausible positions (Zeller et al., 2016) or at various angles (Ide, 2013; Butz et al., 2014). These various conditions, added to the initial synchronous and asynchronous conditions, allowed researchers in the field to further

explore the mechanisms of the illusion. They indicated that the illusion is the strongest in a perfect congruency condition (e.g. synchronous, same-stroking stimulus, same-position etc.) and very weak in conditions of total incongruency (e.g. asynchronous, different stroking stimulus, different position) (Filippetti et al., 2019), but also that there are intermediate levels when the illusion can occur in certain conditions and groups (e.g. vision-only (Rohde et al., 2011), light-only (Durgin et al., 2007), see-touch (Davies and White, 2013)). These findings suggest that there is an interplay between top-down and bottom-up processes which reduce conflicting multisensory input and which may vary at an individual level, this being supported by neurophysiological evidence such as the involvement of higher-order multisensory integration areas such as the premotor cortex and the superior and inferior parietal lobules in the experience of the illusion (Rohde et al., 2011; Zeller et al., 2016). We used some of these conditions such as see-touch and light-only to further explore this phenomenon in vicarious pain responders in relation to the models by Rohde et al. (2011) and Zeller et al. (2016) which emphasise the importance of the various levels of receiving conflicting sensory information.

Seeing someone else in pain activates neural circuitry involved in the physical perception of pain (Jackson et al., 2006; Lamm et al., 2011). However, for a subset of the general population this extends to reportable pain-like experiences evoked by observing others in pain (Fitzgibbon et al., 2010b, 2012; Osborn and Derbyshire, 2010). These individuals have been called vicarious pain responders, or mirror-pain synaesthetes. Ward and Banissy (2015), in their account of mirror-touch/pain synaesthesia, suggest that this may reflect an over-inclusive body ownership mechanism, in which all observed bodies are matched to the person's own internal body model, or as a failure in a top-down orienting mechanism for selective attention to the self that inhibits representations of the (non-self) other. Whatever the precise mechanism, the prediction is that a greater tendency to treat all observed bodies as self-related will result in an increased tendency to experience the RHI, as well as the tendency to report experiences on their own body as a result of observing these on other people (the defining feature of mirror touch/pain).

One study already tested the performance of vicarious pain responders on the RHI using only subjective reports (not proprioceptive drift). Derbyshire et al. (2013) showed a greater tendency to incorporate the rubber hand in the pain-responder group when compared to controls and this effect was unusually apparent for the asynchronous stroking

condition (which tends not to induce the illusion in controls). We extend this to include five different manipulations of the RHI, including conditions in which the dummy hand is observed without any physical touch, and grouping participants via a new assessment tool for vicarious pain experience (Grice-Jackson et al., 2017a).

The Vicarious Pain Questionnaire (VPQ) employs 16 movie clips depicting people experiencing physical pain, and probes the phenomenological characteristics of any felt pain sensations provoked in the observer (e.g. pain quality, pain intensity, pain localisation). Using a bottom-up approach of cluster analysis, three groups are identified: (1) non-responders or controls (who report no pain when watching a video with someone else experiencing physical pain), (2) sensory-localised responders (S/L) (who report a precisely localised feeling of pain at the same location as the person in the video) and (3) affective-general responders (A/G) (who report a generalised and emotional feeling of pain). The validity of these groupings is endorsed by observed difference in structural and functional brain characteristics (Grice-Jackson et al., 2017a,b) and, in the present study, we demonstrate cognitive differences between the groups and provide the first assessment of test-retest reliability of the VPQ. Thus, using the VPQ to group and recruit participants, we tested both subjective and objective measures of the rubber hand illusion, with five different manipulation. Two of these manipulations were the standard synchronous and asynchronous conditions.

Based on published findings (Derbyshire et al., 2013), we predicted that individuals within the responder groups would be less sensitive to asynchrony (i.e. they will show the illusion in both conditions). We had no predictions about whether this effect would be found for one or both responder groups. Two further manipulations involved the visual presentation of touch from a paintbrush or light from a laser pointer in the absence of any physical sensation. Here, our prediction was that the sensory-localised group (who feel sensations in the same location that they observe them on others) would show the RHI illusion, as found for mirror-touch synaesthesia (Davies and White, 2013). The fifth condition involved the reverse scenario of feeling touch while observing an untouched dummy hand. We were not aware of any previous report of this manipulation inducing the RHI, hence, this serves as an important control measure across all groups to assess for a general bias in responding.

2.3 Materials and methods

2.3.1 Participants

Ninety-eight volunteers from the University of Sussex took part in the experiment (70 Females; 28 Males; Aged 18-34 yrs; Mean = 21.75 ± 3.11 SD). Each participant completed the Vicarious Pain Questionnaire (VPQ) and were divided into three groups based on the 2-step cluster analysis performed on the VPQ (see Section 2.3.2 for further description). The groups were: 57 non-responders (29 F; 18 M; Aged 18-34 yrs; M = 21.88 ± 3.45 SD), 22 sensory-localised responders (S/L) (17 F; 5 M; Aged 18-25 yrs; M = 21.6 ± 2.15 SD), and 19 affective-general responders (A/G) (14 F; 5 M; Aged 19 – 33 yrs; M = 21.53 ± 3.1 SD).

Since its development, a total sample of N=1056 individuals (Aged 18-60 yrs, M= 20.42 ± 4.16 SD, 297 Males, 759 Females) have completed the VPQ including data from N=573 reported by [Grice-Jackson et al. \(2017a\)](#). The larger sample also included 82 participants (Aged: 18-33 yrs, M = 20.23 ± 3.31 SD, 68 Females, 14 males) who had taken the measure twice, at least one academic year apart. We used this dataset to undertake an analysis of test-retest reliability of the VPQ and to determine how the group structure is affected by different parameters entered into the clustering model. Cluster analysis is an exploratory analysis that requires large data sets ([Landwehr, 1987](#)) and so was run on the entire sample, and not just the experimental subsample.

2.3.2 Vicarious Pain Questionnaire

Description. The Vicarious Pain Questionnaire (VPQ; developed by [Grice-Jackson et al. \(2017a\)](#)) was run using Bristol Online Survey. The questionnaire comprises 16 videos (no audio) of people experiencing physical pain (e.g. falls, sports injuries, injections), each video lasting for approximately 10 seconds. After each video, participants were questioned about their experience. First, participants were asked if they experienced a bodily sensation of pain while viewing the video (yes/no). If the answer was ‘yes’, participants were asked to describe their pain by answering three more questions about their experience: 1) how intense their pain experience was (1-10 Likert scale, 1= very

mild pain, 10 = highly intense pain); 2) if and where they localised the pain, answering options were either 'localised to the same point as the observed pain in the video', 'localised but not to the same point', and 'a general/non-localisable experience of pain'; 3) to select pain adjectives from a list that best described their vicarious pain experience (10 sensory descriptors such as 'tingling', 'burning', 'stinging', 10 affective descriptors such as 'nauseating', 'gruelling', 'aversive' and 3 cognitive-evaluative descriptors 'brief', 'rhythmic', 'constant').

From these answers, a Localised – Generalised score was computed from the total of 'localised to the same point' and 'localised to a different point' minus the total number of non-localisable (generalised) experiences. A Sensory – Affective score was computed from the total number of sensory adjectives minus the total number of affective adjectives.

Subsequently all participants (regardless of their affirmative or negative answer to the first question) were asked to rate how unpleasant their experience was (1-10 Likert scale, 1 = not at all unpleasant, 10 = highly unpleasant). The final section of the VPQ asked participants if they had previously experienced vicarious pain in their daily life and how regularly that happened (10 point Likert Scale, -5 = hardly ever, 5 = very regularly).

Two-Step Cluster Analysis. The two-step cluster analysis comprised an initial hierarchical cluster analysis using Ward's Method (Ward Jr, 1963) and a second k-means cluster analysis. The cluster centroids and number of clusters for the k-means analysis were provided by the hierarchical cluster analysis. We repeated an earlier clustering approach (Grice-Jackson et al., 2017a) based on three input variables (total number of pain responses, localised-generalised score, sensory-affective score). This analysis was contrasted against two similar models in which total pain responses was substituted for the conceptually related variables of mean intensity of pain responses, or the regularity of pain responses (in daily life).

2.3.3 Rubber Hand Illusion Questionnaire

The RHI questionnaire contained 10 items divided into three subscales: ownership, location, and agency (Longo et al., 2008), see Table 2.1 for further details. The items were measured on a 7-point Likert scale (1 = strongly, 7 = strongly agree). Four extra questions

were added for the light condition, in order to record any tactile or thermal sensations induced by the laser beam (see Table 2.1 for detailed description of the items). These last four questions were added at a later stage and therefore data was gathered only from a subset of participants (N=39).

Table 2.1: RHI questionnaire items and subscales.

Subscale	Items
Ownership	<i>It seemed like...</i>
	1. ...I was looking directly at my own hand, rather than at a rubber hand.
	2. ...the rubber hand began to resemble my real hand.
	3. ...the rubber hand belonged to me.
	4. ...the rubber hand was my hand.
	5. ...the rubber hand was part of my body.
Location	6. ...my hand was in the location where the rubber hand was.
	7. ...the rubber hand was in the location where my hand was.
	8. ...the sensation I felt was caused by the paintbrush touching (or laser pointer playing on) the rubber hand.
Agency	9. ...I could have moved the rubber hand if I had wanted.
	10. ...I was in control of the rubber hand.
Light induced sensations	11. ...I felt a tactile sensation in my hand.
	12. ...I felt a thermal sensation in my hand.
	13. ...the sensation was cold.
	14. ...the sensation was warm.

2.3.4 Experimental procedure

In the RHI task, the participant was seated at a table, opposite to the experimenter with his/her right arm placed in a box ($86cm \times 60cm \times 20cm$). The participants were asked to rest her/his hand in the most comfortable position with the palm facing down and slightly arched. A life-size model of a right hand was placed in the box, directly in front of participant body midline. The participant could only see the dummy hand through a squared hole on top of the box, but could not see her/his own right hand which was occluded by the box cover from the top and by a piece of black fabric from the right-hand side. The distance between participant's right index finger and the index finger of the fake hand was 20cm.

Five conditions were performed in a counterbalanced order across participants: Synchronous (the timing of the brush strokes on the rubber hand and participant's own hand was synchronized); asynchronous (the timing of the brush strokes was out of phase by approximately 625ms); light (a laser beam was playing on the index finger of the rubber hand); see-touch (the brush stimulation was applied only to the rubber hand) and; feel-touch (the brush stimulation was applied only to participant's real hand). At the beginning of each condition, a cover was placed on top of the box and the participant was asked to estimate the location of her/his right index finger tip by reading the corresponding number along a one-meter ruler laid across the setting top, parallel to the frontal plane. The reading was repeated three times before each trial and the placement of the ruler varied each time to prevent the participant repeating responses in subsequent readings. These measurements were followed by 120s stimulation 'induction' at approximately 1.6Hz (75 times in 120s) for all conditions. The paintbrush stimulation was applied from the knuckle to the finger nail, while that of the laser pointer was back and forth from the knuckle to the finger nail as it was not easy to switch off/on and maintain timing. Following this, post-induction finger location judgements were obtained in the same manner as prior to the induction and the participant filled out the RHI questionnaire after each condition. The average of the three measurements taken before and after each trial was calculated. Proprioceptive drift was calculated by subtracting the pre-induction finger location judgement from the post-induction finger location judgement.

$$PD = \text{mean}(\text{post-induction judgements}) - \text{mean}(\text{pre-induction judgements})$$

2.3.5 Data Analysis

The statistical software used was SPSS version 23 (SPSS Inc., USA). The significance level for all analyses was set at $p < 0.05$ and the results reported are two-tailed.

Analyses were performed to test the effects of two independent variables (groups and stimulus type) on two dependent variables (proprioceptive drift and RHI questionnaire subjective ratings). $3(\text{group}) * 2(\text{stimulation mode})$ mixed model ANOVAs were used to analyse the data of proprioceptive drift and each of the RHI questionnaire subscale for the synchronous and asynchronous conditions. For the proprioceptive drift data,

outliers were excluded for each condition using SPSS based on the 3-interquartile range (IQR). Thus, one outlier was excluded from the asynchronous condition, four from the light condition and one from the see-touch condition. No outliers were found in the questionnaire data outside the 3-IQR. Subsequent post-hoc tests adjusted for multiple comparisons (Bonferroni corrections) assessed differences between and within groups. One-way ANOVAs were used for each of the other three conditions to test group effects on proprioceptive drift. On the questionnaire data, non-parametric tests were used for each subscale.

The sample size was based on previous publications using group comparisons in the RHI illusion. The clinical group sizes were represented by about 20 individuals whilst control groups sizes had the same number or larger (Eshkevari et al., 2012; Kaplan et al., 2014; Thakkar et al., 2011; Paton et al., 2012). Power analyses were run on proprioceptive drift data. These indicated a power higher than the conventional accepted power of 0.8 (Murphy et al., 2014) for the synchronous, asynchronous, and light conditions, but lower in the see-touch and feel-touch conditions. Thus, the null results obtained in these last two conditions should be cautiously interpreted.

2.4 Results

2.4.1 Reliability of the VPQ

For the 82 participants who completed this measure on two occasions, the test-retest scores were all significantly correlated between time 1 and time 2 as shown by Spearman's correlations: total pain responses ($\rho = 0.629$, $p < 0.001$); mean pain intensity ($\rho = 0.640$, $p < 0.001$); reported levels of vicarious pain outside of experiment ($\rho = 0.349$, $p = 0.001$); localised-general score ($\rho = 0.295$, $p < 0.001$); and sensory-affective score ($\rho = 0.550$, $p = 0.007$). Correlation coefficients are a measure of effect size and, by convention, values >0.5 are considered large, and those >0.3 are considered medium (Cohen, 1988). The most reliable individual difference measures in psychology, refined over decades of research, tend to have correlations around 0.7 or 0.8 (Vul et al., 2009). Considering the different ways of clustering the data, the inclusion of mean pain intensity led to the most consistent clustering ($\chi^2 = 48.512$, $p < 0.001$; Cramer's $V = 0.544$, $p < 0.001$), fol-

lowed by reported levels of real-world vicarious pain ($\chi^2 = 47.947$, $p < 0.001$; Cramer's $V = 0.541$, $p < 0.001$), and total number of pain responses ($\chi^2 = 37.817$, $p < 0.001$; Cramer's $V = 0.480$, $p < 0.001$). As such, we conclude that the VPQ measure is reliable over time and the reliability is enhanced by adding mean intensity rather than total number of pain responses, although it is to be noted that both methods are adequate and yield only minor differences in the clustering across the whole data set (presented in Appendix A.1).

2.4.2 Proprioceptive drift

Means and standard deviations of proprioceptive drift for each condition and in each group are shown in Table 2.2.

Table 2.2: Mean proprioceptive drift (mm) and standard deviations for each condition in each group.

Group	Conditions				
	Synchronous	Asynchronous	Light	See-touch	Feel-touch
Controls	15.96 \pm 23.38	3.04 \pm 18.54	2.01 \pm 11.50	1.07 \pm 14.40	- 2.98 \pm 14.40
S/L	21.36 \pm 22.72	17.30 \pm 18.46	17.42 \pm 29.13	7.83 \pm 24.35	-1.27 \pm 17.33
A/G	23.51 \pm 19.78	-5.88 \pm 22.51	3.77 \pm 19.15	10.96 \pm 27.08	-1.12 \pm 18.41

Considering first the effect of synchrony/asynchrony, the 2*3 ANOVA used for synchronous and asynchronous conditions showed significant main effects of stimulus type, $F(1, 189) = 20.808$, $p < 0.001$, $\eta^2 = 0.039$ and group, $F(2, 189) = 3.800$, $p < 0.05$, $\eta^2 = 0.099$ on proprioceptive drift. There was also a statistically significant interaction between the effects of group and stimulus type, $F(2, 189) = 3.774$, $p < 0.05$, $\eta^2 = 0.038$, indicating that synchronous and asynchronous stimulations evoked different group effects. Post-hoc tests using Bonferroni corrections set at $\alpha = 0.008$ (i.e. $0.05/6$ (comparisons)) were applied. Significantly greater proprioceptive drift was found in the asynchronous condition in the S/L group when compared to controls, $t(76) = -3.017$, $p = 0.003$, $d = 0.89$ and to A/G, $t(38) = 3.540$, $p = 0.001$, $d = 0.74$. No significant differences were found in the synchronous condition. Differences between synchronous and asynchronous conditions were assessed within the three groups. Proprioceptive drift was significantly greater in the synchronous than in the asynchronous conditions in controls, $t(56) = 4.520$, $p < 0.001$, and in A/G group, $t(18) = 4.723$, $p < 0.001$. However, there was no significant difference in proprioceptive drift in the S/L group, $t(21) = 0.848$, $p = 0.407$. Figure 2.1 shows all these

results. In short, the S/L responder group shows a disruption of body ownership insofar as they have a greater tendency to incorporate asynchronous touch to the dummy hand into their body schema.

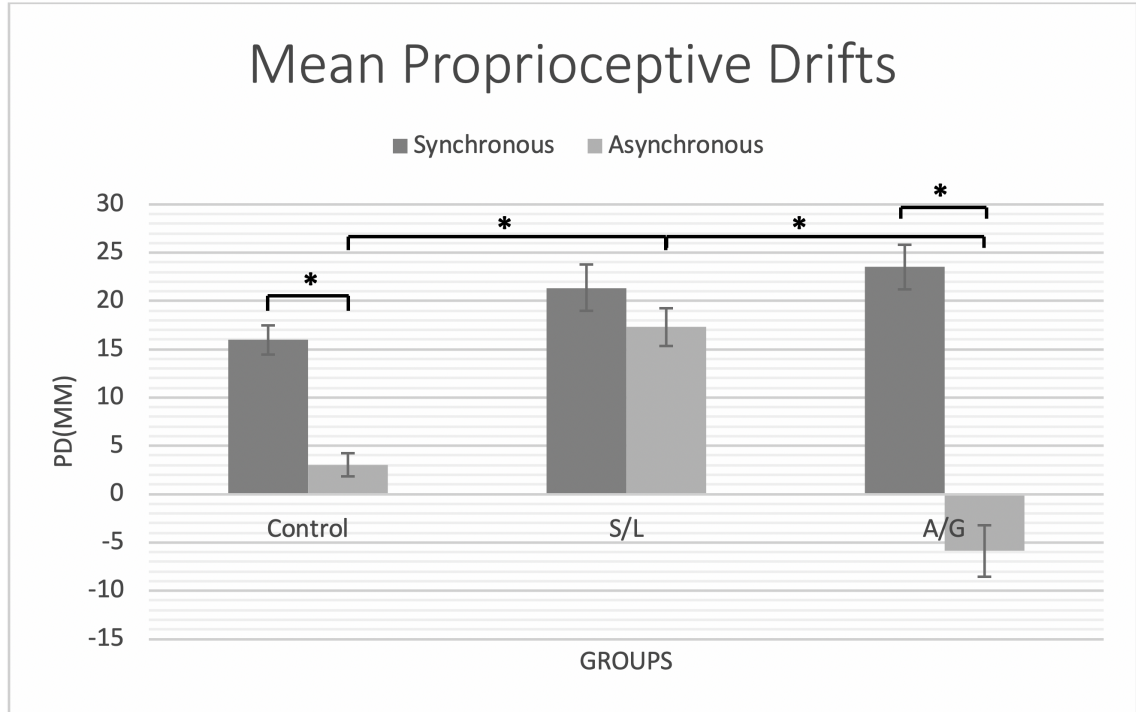


Figure 2.1: Mean PDs (mm) of the three groups for Synchronous and Asynchronous conditions. Error bars indicate one standard error.

The other three conditions were analysed using one-way ANOVAs, as the focus was on differences in between groups, rather than direct comparisons of the conditions. No significant differences were found for see-touch, $F(2,94) = 2.153$, $p=0.122$ and feel-touch, $F(2,95) = 1.231$, $p=0.297$ conditions between the groups. This is important because it suggests that there is not a general tendency to incorporate the rubber hand (or a general response bias) but, rather, a specific tendency to do so under some conditions. There was a significant difference in the light condition, $F(2,92) = 5.601$, $p=0.005$ (results are shown in Figure 2.2). However, this data failed Levene's test for equality of variances and the post hoc Games-Howell test comparing S/L group with controls showed only a trend, $p=0.061$, $d=0.89$. Further exploratory analyses for the light condition can be seen in Appendix A.2.

The results obtained for proprioceptive drift showed higher susceptibility for the illusion in the asynchronous condition in the S/L group which scored higher than the controls and a similar trend was observed in the light condition.

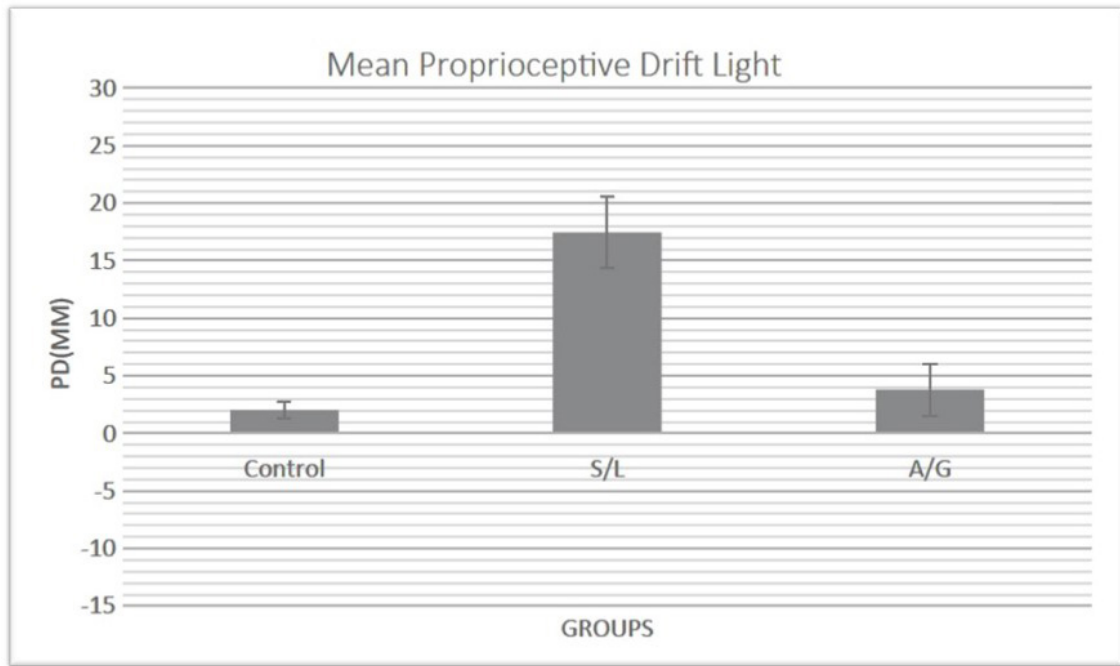


Figure 2.2: Mean PDs (mm) of the three groups for the Light condition. Error bars indicate one standard error.

2.4.3 Subjective ratings

Since almost half of the conditions failed Shapiro-Wilk normality test, each of the three subscales of the RHI questionnaire: ownership, location, and agency were analysed using Kruskal Wallis non-parametric test followed by post-hoc Mann-Whitney test. Significant differences were identified on the ownership subscale in the asynchronous condition ($H(2)=10.257$, $p=0.006$; $S/L > C$, $U=103.0$, $p=0.003$; $S/L > A/G$, $U=103.0$, $p=0.006$) (see Figure 2.3) and see-only condition ($H(2)=6.457$, $p=0.04$; $S/L > C$, $U=412.0$, $p=0.018$) and on the location subscale in the synchronous condition ($H(2)=6.174$, $p=0.046$; $S/L > C$, $U=421.5$, $p=0.024$) (see Figure 2.4). In summary, the questionnaire results show a similar pattern to the proprioceptive drift scores, namely the S/L responder group shows a greater tendency to incorporate the dummy hand.

A subset of participants ($N=39$) were asked about tactile/thermal sensations from the laser light stimulation. Of these participants, 60% agreed to experiencing a sensation on one or more questions, and these did not significantly differ across groups (group percentages: Controls=52%; S/L= 82%, A/G=44%; $\chi^2 = 3.521$, $p=0.172$). Participants who experienced sensations from the laser light reported more subjective illusory experiences in this condition (see Appendix A.3), thus replicating Durgin et al. (2007).

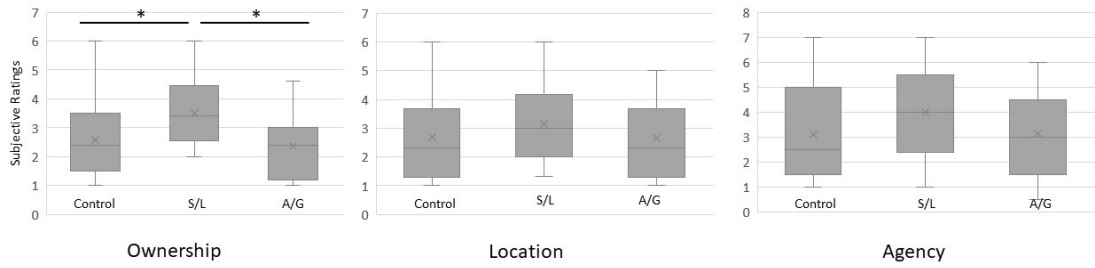


Figure 2.3: Subjective ratings in the asynchronous condition for each sub-scale.

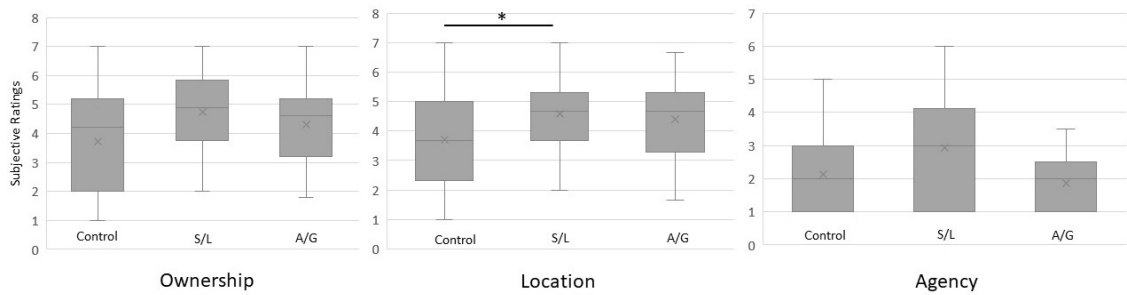


Figure 2.4: Subjective ratings in the synchronous condition for each sub-scale

2.5 Discussion

Previous research has suggested an atypical propensity to experience the rubber hand illusion, a putative measure of body ownership, in people who report experiencing the pain of others (Derbyshire et al., 2013) or who report experiencing touch when seeing others touched (Davies and White, 2013). However, the mechanism behind this is not clear: is it visual capture, or an exaggeration of the normal pattern, or something else?

Here, we used a novel way of identifying and grouping vicarious pain responders (Grice-Jackson et al., 2017a), that divides them into two groups: a sensory/localised (S/L) group who reports localised experiences with sensory qualities on their own body when viewing pain and an affective/general (A/G) group who reports nonlocalised experiences with affective qualities. We show that the S/L group has a distinctive pattern on the RHI, whereas the A/G resembles controls. The S/L group show the RHI for both synchronous and asynchronous stroking (in terms of higher proprioceptive drift and subjective ratings of ownership and agency). Moreover, there was a trend towards higher proprioceptive drift in the light condition, and they also reported greater subjective ratings in the synchronous condition. None of the groups experienced the illusion when the RHI

was broken down into its constituent parts (seeing the dummy touched, the ‘see-touch’ condition; or feeling one’s own hand touched, the ‘feel-touch’ condition). This demonstrates that there is not a general tendency towards incorporating the rubber hand *per se*, nor a general tendency for the RHI to be driven by the sight of touch (as suggested previously for mirror-touch synaesthesia). Together, these results provide evidence that the S/L group have a heightened tendency to incorporate the rubber hand within their own body representation under certain conditions. The question as to why it is found for the S/L group alone remains to be determined. Of relevance here is that the S/L group, but not the A/G group, report that their experiences are localised to the corresponding body part at least when reporting vicarious pain (and this is supported by more somatotopic activity in primary somatosensory cortex in the S/L group; (Grice-Jackson et al., 2017a)). Either difficulties in body ownership are limited to the S/L group or, else, difficulties in body ownership are common to both but operate on different levels (whole bodies, v. body parts) and generate different effects depending on the nature of the paradigm (e.g. rubber hand illusion v. whole body illusion; (Lenggenhager et al., 2007)). In the sections below we discuss the results in detail. Firstly, in relation to previously reported individual differences and group based differences in the RHI. Secondly, we discuss our findings in relation to theoretical models of the RHI.

2.5.1 Previous atypical findings in the RHI

Previous literature has documented atypical RHI susceptibility patterns in clinical conditions including eating disorders, schizophrenia, and autism and our results will be discussed considering similarities or dissimilarities with these conditions.

Our results resemble findings that have been previously reported in the eating disorder literature. Patients with diagnosis of body dysmorphic disorder present no differences in proprioceptive drift between the synchronous and asynchronous conditions, scoring significantly higher in both conditions than in the recorded baseline (Kaplan et al., 2014). Eshkevari et al. (2012) found that patients with anorexia nervosa score higher on both proprioceptive drift and on overall subjective ratings when compared to controls and Zopf et al. (2016) reported higher subjective ratings in anorexia nervosa for both synchronous and asynchronous RHI conditions when compared to controls, al-

though they didn't find it in proprioceptive drift. The pattern of results in our group is similar to these findings which may be due to abnormalities in self representations. Eating disorders have been associated with a more unstable bodily self-representation and increased bodily plasticity (Eshkevari et al., 2012; Kaplan et al., 2014) as well as interoceptive deficits ((Preyde et al., 2016), but also see (Eshkevari et al., 2014)). Lower interoceptive awareness is associated with increased susceptibility to RHI and with a less clear perception of internal bodily processes that give rise to the bodily self (Tsakiris et al., 2011), but also see (Crucianelli et al., 2018) and dysfunctionalities within the insular cortex have been linked to distorted body-perceptions (Heydrich and Blanke, 2013) and to eating disorders (Strigo et al., 2013). Comparatively little is known about these mechanisms in vicarious pain responders, although the insula is also implicated. Grice-Jackson et al. (2017a) reported increased grey matter density in the insula in both S/L and A/G responders and, using fMRI functional connectivity, found greater coupling of the insula with the right temporo-parietal junction (a region implicated in selectively attending to self v. other) in the S/L group when viewing the pain of others (Grice-Jackson et al., 2017b). Insula dysfunction could therefore explain the tendency for the S/L group to have a greater RHI (found in several conditions for subjective ratings), although it does not make specific predictions about the asynchronous condition. It does, however, make the testable prediction that eating disorders and these differences in vicarious pain perception may co-occur more than chance if they share similar neurocognitive mechanisms.

The heightened tendency towards experiencing the RHI has also been associated with more pronounced psychotic traits, but, this manifests itself as an exaggeration of the normal (synchronous) effect (Germiné et al., 2013; Kállai et al., 2015). In one study, schizophrenic patients scored higher on ownership questions of the RHI questionnaire and presented greater proprioceptive drift after the synchronous condition (Thakkar et al., 2011). Overall, psychotic traits seem to be associated with more pronounced subjective feelings of ownership, but only after the synchronous condition of the rubber hand illusion and these results are not convincingly replicated for proprioceptive drift. Compared to this group, our S/L subjects present some similarities (i.e. higher subjective ratings of ownership than controls in synchronous condition) but differ insofar as this extends to the asynchronous condition. Conversely, lower susceptibility towards

the RHI (in the standard synchronous condition) has been found in people with Autism Spectrum Conditions (ASC) or high autistic traits in non-clinical groups. This is expressed in measures of proprioceptive drift (Palmer et al., 2013) and in reported experience of ownership, when there is no discrepancy between the felt and seen location (Paton et al., 2012). In terms of theoretical models, it is possible that people with autism rely more on sensory input (from their own hand) and less on a top-down internal model of the body (Quattrocki and Friston, 2014). A reverse mechanism may be present in the S/L group and we will discuss possible explanations for this below.

2.5.2 Theoretical models explaining the RHI

Three models explaining the occurrence of the illusion have been proposed until now so we will further interpret our results within these theoretical models. The first, classical model proposes that the RHI is enhanced by synchrony or, more generally, by matching external signals (tactile, visual, and proprioceptive). The Botvinick and Cohen (1998) model suggests that the visuo-tactile correlation alone is responsible for updating the spatial location of subject's real hand and that intermodal matching is a sufficient condition for the rubber hand attribution. This model has been expanded arguing that the visuo-tactile correlation is necessary but not always sufficient. It has been proposed that not only the matching of external stimuli is important but also the matching between the external input and the pre-existing body image (e.g. body shape/size) or body-schema (e.g. body configuration) (Makin et al., 2008; Tsakiris, 2010). Even though the visual-tactile synchrony is the main driver of the illusion, the coherence with pre-existing visual and proprioceptive body representations is necessary for the illusion to manifest. Thus, there is a necessity of congruent posture and identity with respect to the participant's hand (Tsakiris and Haggard (2005), but also see Holle et al. (2011)) which facilitates the integration of sensory information in favour of vision within the peripersonal space (Makin et al., 2008). In our study, we did observe that the illusion occurred when there was a match between visual and tactile input (synchronous condition) in all groups, however the S/L group performed similarly in the asynchronous condition too. Within this model, we would conclude that the S/L interprets asynchrony as a matching signal. This could be because they do not perceive the visuo-tactile asynchrony (a very unlikely

scenario since the temporal difference was of approximately 625ms) or, more likely, that the asynchrony is perceived but does not influence the computation of body ownership in the normal way. For instance, it is to be noted that both the visual and tactile signals are equally correlated in both the synchronous and asynchronous conditions. Whereas they are in-phase in the synchronous condition (occur simultaneously) they are out of phase (occur consecutively) in the asynchronous condition (i.e. correlations of +1 and -1 respectively). In our ‘see touch’ condition the dummy hand was touched and in our ‘feel touch’ condition the real hand was touched; i.e. there was never a correlation between them. It may be that the S/L group are sensitive to visuo-tactile correlations, whereas the more typical pattern is to rely also on visuo-tactile simultaneity. This generates a testable prediction that asynchronous stroking in which the strokes occurs unpredictably (i.e. with zero correlation) would not lead to the RHI in the S/L group.

A second model that has been proposed by Rohde et al. (2011) states that the RHI is disrupted by asynchrony rather than enhanced by synchrony or matching signals. Their study found that visual capture alone (i.e. looking at the dummy hand with no touch to either hand) produced comparable proprioceptive drift to the synchronous condition. The authors proposed that proprioceptive drift is typically found when looking at an anatomically plausible dummy hand and that the asynchronous control condition has a negative effect on the visual capture of proprioception as opposed to the synchronous condition having a positive effect on visual-proprioceptive integration. Within this model’s framework, our result shows that asynchronous stroking does not weaken the visual-proprioceptive integration in the S/L group suggesting that this group is not treating the visuo-tactile signals as mismatching. The main condition that adjudicates between this model and the previous one is whether there is drift in the absence of any touch to either hand. Our study did not include this condition and it is important for future research to explore this with these groups and in terms of other individual differences.

A third theoretical model, the predictive coding or Bayesian framework, proposes that the rubber hand illusion can be construed as the interpretation that different sensory signals (tactile, visual, proprioceptive) have a common cause, i.e. that the signals are attributed to a single hand rather than two different causes namely a dummy and a real hand (see (Samad et al., 2015)). The attribution of a common cause depends on two

things: the nature of the incoming sensory signals (e.g. how well they are matched) and prior expectations (e.g. how long it takes for an observed touch to be felt). With regards to the sensory signals, those that are spatially and temporally aligned are more likely to be integrated (i.e. attributed to a common cause) – as in the original [Botvinick and Cohen \(1998\)](#) explanation and other models in that tradition. However, there is an additional property of the sensory signal that is relevant namely it's precision. More precise sensory signals are weighted more heavily, so vision with its high spatial precision tends to dominate over proprioception and, hence, the illusion as measured by proprioceptive drift can occur just by looking at the rubber hand ([Rohde et al., 2011](#); [Samad et al., 2015](#)). This may also be a source of individual differences: if an individual has poor proprioception abilities then they should show a stronger influence of vision and a greater RHI. This is a testable prediction that could account for some of the reported differences including those we observe for the S/L group (note: previous studies on the RHI measure proprioceptive drift rather than actual proprioceptive ability). The alternative, not yet considered in detail by these models, is that there are individual and group differences in priors (i.e. willingness to attribute different signals to a common cause, or to update priors on the basis of new evidence). These kinds of differences have been postulated in conditions such as autism ([Van de Cruys et al., 2014](#)) and schizophrenia ([Fletcher and Frith, 2009](#)) that also show differences in RHI susceptibility, and may also be the case in those who report experiencing the localised pain of others.

2.6 Conclusion

We have identified a new group of individuals who are highly susceptible to the rubber hand illusion. Our findings indicate particularities in body representations and self-other distinctions. The S/L group scored higher under certain conditions on both proprioceptive drift, a measure attributed to body perception and localization. Moreover, the S/L group scored higher on subjective ratings of the illusion. Even though the exact mechanisms are still unknown, there are various possible interpretations. These are not mutually exclusive and include: more unstable body image and body schema, predominant influence of visual input and lower tactile precision. Further research is needed to disentangle these aspects.

Article II: Atypical susceptibility to the Rubber Hand Illusion and Enfacement Illusion in Sensory-Localised Vicarious Pain Responders. Evidence for greater influence of tactile-temporal predictions.

3.1 Abstract

Individual differences in experiencing the pain of others is linked to differences in the sense of body ownership as revealed by the rubber hand illusion paradigm (RHI). Specifically, people who report localised vicarious pain experiences (sensory-localised responders) experience the RHI during asynchronous visuo-tactile stroking as well as synchronous. This atypical pattern is examined further in this study according to the Bayesian Sensory Inference Model in which computations of body ownership depend on the degree (and precision) of sensory evidence, rather than synchrony per se. Sensory-localised responders only exhibit the RHI in asynchronous conditions when the stroking is predictable (alternating) but not when it is unpredictable (random), suggesting individual differences in the way that sensory evidence is weighted. There was no evidence that their bottom-up proprioceptive signals are less precise. Moreover, the enfacement illusion paradigm (EI) was also employed in order to establish performance on a conceptually related bodily illusion paradigm that involves a completely different response judgment (based on vision rather than proprioception). Sensory-localised responders show a comparable pattern on this task consistent with the idea that they have top-down (prior) differences in the way body ownership is inferred, independently of the exact judgment being made.

3.2 Introduction

3.2.1 Bodily ownership. An overview of the rubber hand illusion (RHI) and enfacement illusion (EI) paradigms

The sense of self primarily arises from the feeling of owning one's body. Bodily ownership is one fundamental dimension of the bodily self and represents the capacity to attribute our physical body and the sensations associated with it to ourselves (Costantini, 2014; Tsakiris, 2017). Notably, this dimension is malleable, and the experience of our bodily self is not always as solid and coherent; it can be restricted as it happens in cases of somatoparaphrenia when the ownership over one's limb or part of the body is denied (Feinberg et al., 2010) or expanded to incorporate parts of extraneous bodies (Botvinick and Cohen, 1998; Tsakiris and Haggard, 2005; Tsakiris et al., 2008) or full bodies (Blanke and Metzinger, 2009).

Rubber Hand Illusion

The most popular paradigm proving the malleability of bodily ownership is the rubber hand illusion (RHI) (Botvinick and Cohen, 1998). In this paradigm, participants tend to report that they feel ownership over a dummy hand thus expanding their own bodily boundaries. The paradigm consists of placing a dummy hand in front of the participants whilst their real hand is hidden from view. Subsequently, both hands are stroked either synchronously (at the same time) or asynchronously (out of phase) and most evidence shows that the illusion is stronger in the synchronous condition (Botvinick and Cohen, 1998; Tsakiris and Haggard, 2005). The illusion is reflected in an objective measure of proprioceptive drift, when participants report that the real hand is positioned closer to the rubber hand, and a subjective measure of self-report when participants report their perceived experience of ownership, self-location or agency over the fake hand.

The initial synchronous and asynchronous conditions have represented the main configuration of the RHI, but it has also known many variations along the time. These variations included the introduction of new conditions such as: vision-only when participants have to look at the dummy hand and no stroking is involved (Rohde et al., 2011;

Samad et al., 2015); light condition when a laser beam plays on the dummy hand (Durgin et al., 2007); or conditions when only one of the hands is stroked: either the dummy hand with no touch on the real hand (Davies and White, 2013), or the real hand with no strokes on the dummy hand (Botan et al., 2018b). The illusion is the strongest in the synchronous condition as indicated by proprioceptive drift and subjective ratings, but it can also occur in other conditions such as vision-only (Rohde et al., 2011; Samad et al., 2015) or light (Durgin et al., 2007). Other manipulations consisted in changes in the appearance (e.g. skin colour) of the dummy hand (Farmer et al., 2012; Lira et al., 2017) or variations of the angle of the dummy hand in respect to the real hand and of perspective (Bertamini et al., 2011; Ide, 2013; Holle et al., 2011), of the distance between the dummy hand and participant's body (Preston, 2013), and of the timing of the strokes (Shimada et al., 2009; Costantini et al., 2016). Regarding the latter one, previous studies have indicated that the strength of the illusion in the asynchronous condition is negatively correlated with the delay time between the strokes. The effect of the illusion is very strong for delays shorter than 300ms and it is significantly attenuated by delays larger than 600ms (Shimada et al., 2009). These results are compatible with the view that the brain requires temporal contiguity of 200–300 ms to integrate visual and tactile/proprioceptive inputs for self-body processing (Shimada et al., 2010). Moreover, the attenuation is seen both in proprioceptive drift and subjective ratings measures (Shimada et al., 2014) and it depends on participants' temporal sensitivity (i.e. their ability to consciously detect temporal discrepancies) (Costantini et al., 2016). These later findings may explain the great variability seen in the RHI and the fact that the correlation between visual and tactile signals within certain time limits can be integrated together and inferred to a common cause which, in some people at least, can elicit the RHI (Fujisaki et al., 2004; Parise et al., 2012).

There have been various interpretations of these findings and the mechanisms that contribute to the illusion. The main theoretical explanation states that the RHI arises mainly from the integration of proprioceptive, visual and somatosensory inputs which are processed according to the internal body representation, the illusion being stronger when the external inputs match each other but also the internal representation of the body (Costantini and Haggard, 2007). There is a large body of evidence supporting this theory, with various studies proposing that the illusion is enhanced by synchrony, when

there is a complete match between all sensory signals: vision, touch, and proprioception (Botvinick and Cohen, 1998; Tsakiris and Haggard, 2005). Further evidence also suggested that the illusion is stronger when the rubber hand looks similar, has same orientation and side as the real hand (e.g. both left or both right) and when the hand is within the peripersonal space (PPS) of the person (Tsakiris and Haggard, 2005; Preston, 2013; Makin et al., 2008). Thus, the occurrence of the RHI seems to depend on an interplay between bottom-up (i.e. external inputs) and top-down (i.e. previous body model) inferences integrated in higher order multimodal areas (Ehrsson et al., 2004; Tsakiris et al., 2008; Ishida et al., 2015; Limanowski and Blankenburg, 2015). Notably, the illusion also occurs in the absence of any direct tactile stimulation, in the vision-only condition by simply looking at the dummy hand (Rohde et al., 2011; Samad et al., 2015) or in the light condition by projecting a laser beam on it which usually elicits a thermal sensation on the real hand (Durgin et al., 2007), the results in proprioceptive drift being comparable to the ones obtained in the synchronous condition. This evidence suggests that the RHI is more likely to be disrupted by asynchrony rather than enhanced by synchrony. However, since there is no mismatch between the sensorial inputs in the above-mentioned conditions, the claim that the illusion is stronger when there is a match between the external and internal inputs remains legitimate.

In the attempt to further elucidate these claims, Samad et al. (2015) applied the Bayesian causal sensory inference model to stimulus integration in the RHI. This framework sustains that the RHI derives mainly from the perception of a common cause for proprioceptive, tactile and visual sensations and applies a causal inference process to it. Thus, the Bayesian causal inference model would make an inference of the possible common cause of the experience based on the prior probability of the cause (e.g. the probability that the touch that I feel on my real hand is caused by the touch that I see on the dummy hand) in which case, the properties of the stimulus including location and time will be approximated according to the inferred cause. In the synchronous and asynchronous conditions of the RHI, there are three modalities (i.e. vision, touch, and proprioception) contributing to the experience which can be integrated based on the attribution of a common cause and two signals (i.e. spatial and temporal) deriving from these three modalities. Moreover, the model would generate optimal estimates of location and time and their match with the actual input signals would result in a greater

likelihood of attributing a common cause, as it usually happens in the synchronous condition but not in the asynchronous condition when there is a temporal delay. In the vision-only condition, there are only two modalities (i.e. vision and proprioception) and one signal (i.e. spatial) involved in the illusion but, within this model, more precise sensory signals are weighted more heavily (Ernst and Banks, 2002). Thus, vision which is a highly precise and extremely reliable sensory signal can override proprioception, a weaker input, making possible the occurrence of the illusion in the vision-only condition (Rohde et al., 2011; Samad et al., 2015). As such, this model clarifies and reconciles findings obtained when manipulating the RHI with various conditions including synchrony, asynchrony or vision-only. In our study, we used this model to make further predictions about possible causes of atypical susceptibility to the RHI observed in vicarious pain responders as further explained in the Section 3.2.2.

Enfacement Illusion

A second paradigm that has been widely used to investigate the bodily self is the enfacement illusion (EI), a facial analogue of the RHI, which uses tactile facial stimulation to manipulate the perceived similarity with ‘the other’. EI further exploits integration of multisensory signals such as vision and touch to update the internal mental representation of self-appearance and, besides generating a greater feeling of ownership over an extraneous body part (i.e. the face), it also acts on mnemonic mechanisms of face-recognition and induces a new sense of identity (Tsakiris, 2008).

During the EI, touch is delivered to the participants’ face whilst they watch an induction video presenting mirrored touch delivered to an unfamiliar model’s face (Tsakiris, 2008; Sforza et al., 2010). The touch is delivered synchronously or asynchronously and before and after each induction video measures of perceived similarity between the participant and the model are taken. Participants judge if the morphed faces that they see containing different percentages of themselves and the model look more like themselves or not. Synchronous touch usually generates an increase in perceived similarity when compared to the asynchronous one with participants recognising images that contain a higher percentage of the model as self. They also report feeling greater ownership and agency over and higher similarity to the model’s face (Tajadura-Jimenez et al., 2011).

This pattern of results further suggests that body representations of the self, including appearance and facial features, are malleable and constantly updated by integrated multisensory experiences and that selfhood emerges from the match between first-hand experience, observed actions, and felt sensations.

There have been many alterations of the EI, some of them concerning the induction video, some others concerning the morphing procedure. The original EI study used touched on a morphed face for the induction video (Tsakiris, 2008) whilst a following study did not use a video, but a confederate placed in front of the participant (Sforza et al., 2010). More recent studies used induction videos recording the face of the model being stroked (Tajadura-Jimenez et al., 2011; Maister et al., 2013), this being the option we opted for due to its robustness and simplicity. Regarding the morphing procedure, this also varied from displaying morph videos that participants had to stop whenever they believed that the face looked more like the self (Tsakiris, 2008; Tajadura-Jimenez et al., 2011) or presentation of morphed faces in increments of 1% or 2% that participants had to judge as looking more like the self or like the other (binary decision) (Tajadura-Jimenez et al., 2011; Maister et al., 2013) or using a VAS scale for perceived resemblance with the morph (continuous decision). We opted for the presentation of 2% increment morphs and a binary decision of resembling more self versus other. Regardless of the procedure, all studies provided evidence that synchrony had a stronger effect on perceived similarity than asynchrony.

In this study, the EI complements the RHI and adds two important aspects to it in relation to vicarious pain. Firstly, it explores the ability to identify with the other and to expand ownership over a face and not only a hand by re-adjusting mnemonic facial representations. Secondly, it serves to clarify the role of proprioception (a main component of multisensory inputs in the RHI that lacks in the EI) in the susceptibility to bodily-ownership paradigms in a group of vicarious pain responders as further clarified and explained in the next section.

3.2.2 Bodily ownership and vicarious pain

There are noticeable differences in the susceptibility to bodily ownership paradigms, with certain sub-groups of the population being susceptible to a higher or a lesser degree.

Notably, differences in susceptibility to bodily ownership illusions have been registered in vicarious sensory responders, people who report a sensorial bodily response when seeing others enduring tactile stimulation such as touch or pain (Davies and White, 2013; Derbyshire et al., 2013; Botan et al., 2018b). This phenomenon has been mainly attributed to overreactive sensory mirroring mechanisms and to shared self-other representations (Ward and Banissy, 2015) which may lead to a tendency to treat the other as the self to the point of expanding self-bodily ownership over the other. Indeed, previous research has shown that vicarious sensory responders have a greater susceptibility to bodily ownership illusions. For instance, mirror-touch synaesthetes (MTS) report greater ownership than controls in the RHI paradigm when touch is delivered exclusively to the dummy hand (Davies and White, 2013). Analogously, when observing touch on somebody else's face in an adapted version of the EI, MTS feel touch on their own face but also blur the boundaries between self and other and consider that the other resembles more themselves (Maister et al., 2013).

In this paper, we will focus on vicarious pain responses, the ability to report a conscious bodily feeling of pain when seeing others in pain and which characterize almost 30% of the population (Grice-Jackson et al., 2017a). Based on previous research, we used two different groups of vicarious pain responders which were classified accordingly to the quality of pain felt. Thus, in our experiment we had: a control group or non-responders, people who do not report any bodily sensation of pain when seeing other in pain and represent about 70% of the population; a group of sensory-localised pain responders (S/L), people who report feeling a bodily sensation of pain when seeing others in pain which is localised and has sensorial qualities and represent approximately 17%; and a group of affective-general pain responders (A/G), people who report feeling a bodily sensation of pain when seeing others in pain which is generalised and has affective qualities and represent approximately 10% of the population. A vicarious pain questionnaire was used in order to group the participants (please see Grice-Jackson et al. (2017a); Botan et al. (2018b) for further details).

Atypical patterns of susceptibility to the RHI have already been recorded in vicarious pain responders. Derbyshire et al. (2013) used the RHI paradigm and reported a greater tendency to incorporate the rubber hand in the pain-responder group when compared to controls but they only used subjective reports and did not differentiate the vicari-

ous pain responders in two groups based on the quality of the pain felt. In a more recent study, [Botan et al. \(2018b\)](#) showed that only the sensory-localised group of vicarious pain responders displayed a greater tendency to incorporate the rubber hand in both synchronous and asynchronous conditions as recorded by subjective ratings and proprioceptive drift. Moreover, there was a greater tendency to incorporate the rubber hand in the light condition but not in the see-only condition, when the stroking was applied only to the dummy hand, results that differ from the ones obtained by [Davies and White \(2013\)](#) in MTS. Thus, there seems to be a tendency in S/L vicarious pain responders to be more susceptible to the RHI, a characteristic present in MTS too, however, there are differences in the performance on certain conditions. More specifically, S/L responders perceive asynchrony as synchrony in the RHI and they also have a stronger tendency towards greater ownership when a light beam touches the dummy hand, likely eliciting tactile and thermal sensations on the real hand ([Durgin et al., 2007](#)). However, this is not a general tendency to incorporate the rubber hand since it does not occur in conditions such as seeing the dummy hand being stroked or receiving touch only on the real hand (see [Botan et al. \(2018b\)](#)). Moreover, it is unlikely that the S/L responders are susceptible to the asynchronous condition because they do not perceive the time-delay. As previously mentioned, delays of 600ms (i.e. used in the current studies) severely disrupt the illusion ([Shimada et al., 2009, 2014](#); [Costantini et al., 2016](#)). As such, it is more likely that their susceptibility is due to temporal correlations between the timing of the strokes (e.g. [Ehrsson et al., 2004](#); [Samad et al., 2015](#)). In other words, S/L responders have a greater propensity towards recalibrating predictable lagging sensory signals in order to be consistent with an internal model of common cause ([Fujisaki et al., 2004](#); [Parise et al., 2012](#)), a possibility which will be further investigated in the present study.

In the present study, we try to further elucidate this atypical pattern of performance on the RHI within the Bayesian sensory inference model. As previously explained, this framework proposes that the experience of the RHI derives from integrating incoming sensory signals by attributing a common cause to them based on prior probabilities. Thus, signals which are spatially and temporarily matched are more likely to generate the illusion since they have a higher likelihood to be integrated and to correspond to prior expectations ([Samad et al., 2015](#)). Concomitantly, it also emphasizes the importance of the precision of sensory signals and, according to the Bayesian model of sensory

inference, more precise sensory signals such as vision outweigh proprioception. As such, the illusion would occur just by looking at the hand (in the vision-only condition) but the synchronous condition, consisting in a perfect match between all inputs, would provide the strongest evidence for the illusion.

By applying this model to the atypical performance of sensory-localised vicarious pain responders on the RHI, namely greater susceptibility to the illusion in the asynchronous and/or light conditions, a few explanations can be formulated. Firstly, this group may weigh visual input more than proprioceptive input either because they rely more on visual capture or because they have higher proprioceptive imprecision than the other groups (a probable but unlikely scenario considering the fact that they do not report higher drifts in the see-only condition). Secondly, this group may rely more on the perfect correlation between visual and tactile signals (in the asynchronous condition, the strokes on the real hand are always delivered at a specific time after the strokes on the dummy hand) inducing more easily the perception of a common cause and recalibrating visual-tactile temporal synchrony (Fujisaki et al., 2004; Parise et al., 2012). Thus, an asynchronous random condition, when the touch would be delivered at unpredictable times would strongly disrupt the illusion in all groups.

Starting from these premises, our hypotheses regarding why the S/L group may present the atypical pattern of performance on the illusion, perceiving asynchrony as synchrony were: a) they rely more on visual capture, thus showing higher drift in the vision-only condition when compared to the other two groups; b) they have higher proprioceptive imprecision, easily overwritten by visual capture so they would show higher proprioceptive imprecision when compared to the other two groups; or c) they rely more on prior expectations regarding the time when the touch is delivered thus they would not be susceptible to the illusion in an asynchronous random condition when the touch is delivered randomly, at unpredictable times.

In order to address this, two more conditions and one extra measure were added to the paradigm. Thus, alongside the synchronous and asynchronous conditions, a vision-only condition, a measure of visual capture, and an asynchronous random condition were used. In the vision-only condition, participants had to simply look at the dummy hand for two minutes. In the asynchronous-random condition, participants received alternating strokes on either the real or the dummy hand but at different time intervals

so they could not predict when the next stroke would be delivered. The new measure introduced consisted in taking three reported measurements of the position of the real hand before every condition, without any other previous manipulation, generating a total of twelve measurements. The variation in these measures was calculated providing an indicator of the proprioceptive imprecision (the higher the variation, the higher the imprecision) and, according to our predictions, this would be higher in the S/L group and would positively correlate with proprioceptive drift amplitude.

Besides the RHI paradigm, the EI paradigm was used to determine if the S/L group of vicarious pain responders tends to identify more with someone else's visual features. We hypothesised that, if the performance of the S/L group is not disrupted by asynchrony, then they would identify more with the model in the asynchronous condition too. Moreover, the greater susceptibility to the EI would indicate that proprioceptive imprecision, a crucial component of integrated inputs in the RHI but not in the EI, cannot be the only or main factor contributing to their atypical performance and that this group would also be more prone to identify with another person and not only to incorporate an extraneous body part. As such, this group may have difficulties in accurately inferring selfhood, irrespective of whether they are making self-related proprioceptive or visual appearance judgments.

3.3 Materials and Methods

3.3.1 Participants

A total of 59 participants (mean age = 22.28, SD = 4.53; 49 females) completed the study. Participants were recruited via email invitation or via SONA from Sussex University, and all but four (two S/L and two A/G) had never taken part in our previous research (Botan et al., 2018b). Ethical approval was obtained from the Science and Technology Research Ethics Committee of the University of Sussex and all participants offered their written informed consent at the beginning of the study.

Each participant had previously completed the VPQ online via Qualtrics Online Survey and were divided into three groups following a cluster analysis conducted on a larger dataset of participants (Aged 18–60 years, mean age = 20.11, SD= 6.94; 290 Males, 1004

Females). There were 27 participants classed as non- responders (i.e. controls) (mean age = 23.26, SD = 5.64, 19 females), 20 participants classed as sensory-localised (S/L) responders (mean age = 21.52, SD = 3.62, 17 females) and 12 participants classed as affective-general (A/G) responders (mean age = 21.42, SD = 2.64, 11 females). The groups did not differ by age ($F(2,57) = 1.144$, $p = 0.326$, $\eta^2 = 0.039$) or gender ($\chi^2 = 2.351$, $p = 0.309$).

In the rubber hand illusion task, 8 participants (6 controls and 2 S/L) lack measurements for proprioceptive variance and the asynchronous random condition which were introduced at a later time. Due to technical and logistical issues, 7 participants (4 controls and 3 S/L) did not complete the EI task.

3.3.2 Vicarious Pain Questionnaire (VPQ)

Before completing the tasks, all participants undertook the VPQ. They watched 16 videos (no audio) of people experiencing physical pain (e.g. falls, sports injuries, injections) (Grice-Jackson et al., 2017a). After each video, they had to report :1) if they experienced a bodily sensation of pain;2) how intense was the pain (1-10 Likert scale); 3) if the pain was localised to the same place, to a different place or generalised to the entire body; 4) asked to describe the pain selecting various pain adjectives. These answers were used to generate the three variables (i.e. pain intensity, localised-generalized responses, and sensory – affective responses) entered the two-step cluster analysis. The three groups of vicarious pain responders were generated: controls or non-responders, sensory-localised (S/L) and affective general (A/G) (for further details see Botan et al. (2018b)).

3.3.3 Rubber Hand Illusion

In the RHI task, participant's right arm was placed in a box (86cm * 60cm * 20cm), hidden from view and a visible life-size model of a right hand was placed in the box, directly in front of participant body midline. The stroking was applied to the index finger and the distance between participant's right index finger and the index finger of the fake hand was 20 cm. Four conditions were performed in a counterbalanced order across participants: synchronous (the timing of the brush strokes on the rubber hand

and participant's own hand was synchronized); asynchronous (the timing of the brush strokes was out of phase by approximately 625ms); vision-only (no stroking at all, the participants had to look at the rubber hand for 2 minutes) and asynchronous random (the timing of the brush strokes was out of phase, but this time was completely random; the participants could not predict when the next stroke would start). At the beginning of each condition, the participant was asked to estimate the location of her/his right index fingertip three times by reading the corresponding number along a one-meter ruler laid whose position varied each time to prevent the participant repeating responses in subsequent readings. This generated 12 baseline location measurements (three for each of the four conditions). The standard deviation was calculated for each participant across the 12 measurements, giving an estimation of the variation in proprioception.

Post-induction finger location judgements were obtained in the same manner as prior to the induction. Proprioceptive drift was calculated by subtracting the average of the pre-induction finger location judgements from the average of post-induction finger location judgement:

$$PD = \text{mean}(\text{post-induction judgements}) - \text{mean}(\text{pre-induction judgements}).$$

After each condition, participants completed the RHI questionnaire comprising 10 items divided into three subscales: ownership, location, and agency (Longo et al., 2008), see Appendix B.1, Table B.1 for further details. The items were measured on a 7-point Likert scale (1=strongly disagree, 7=strongly agree).

3.3.4 Enfacement illusion (EI)

The EI task comprised 120s-long clips recording the face of a model being stroked on the right cheek with a cotton bud at a frequency of approximately one stroke per second. There were four models: two females and two males and digital photographs of their faces were taken and subsequently edited on Photoshop CS6, having all non-facial attributes (i.e. hair, ears etc.) removed and a uniform grey background replacing the original one. Both clips and photographs were in black and white and the models had a neutral face-expression. The models and participants were gender-matched and all models were Caucasian (N.B. race does not seem to influence the illusion (Bufalari et al., 2014)).

Prior to the experiment, a photograph of the participant face was also taken and ed-

ited following the same procedure as the models' photographs. Subsequently, the participant face was morphed into the model face using the Abrasoft FantaMorph5 software. The procedure generated morphs of 2% increments in which the participant face was merged with the model face resulting in 50 pictures per model (Sforza et al., 2010). The morphs used in the task varied between 30% and 70% resulting in a total of 21 morphed pictures, the first picture representing 30% model's face and 70% participant's face and the last picture the reverse.

The experiment consisted of two blocks: the synchronous block when the participant face was stroked simultaneously with the model's face and the asynchronous block when the strokes on the participant face alternated with the ones on the model's face, by a delay of approximately 500ms.

During the experimental procedure, the participants first performed a self-recognition task when they saw the 30% to 70% increment morphs in a randomized order and had to judge if the face depicted 'looked more like their own face or like the other person's face'. They were instructed to make their decision using the arrows on the keyboard, with left arrow key corresponding to 'more like myself' and right arrow key corresponding to 'more like the model's face'. Subsequently, they watched the 120s induction clip with their face being stroked synchronously or asynchronously with the face of the model. The clip was presented three times per block and the self-recognition task was performed at the beginning of each block as a pre-induction (baseline) measurement and after each trial (i.e. video presentation) as a post-induction measurement. Thus, each block consisted of a baseline measurement and three trials (i.e. the participants watched the clip three times for each condition). Only one model was used for each block and the block and model order was counterbalanced. A detailed representation of the task can be seen in Figure 3.1.

For each self-recognition task, the point of subjective equality (PSE), representing the point when the participants cannot distinguish between self and other, was calculated using a logistic function (Bacaër, 2011). The logistic function was applied to the percentages of the morph data (x values) generating binary probabilities of y fitted values (Cramer, 2002). The x value corresponding to the minimum value of the sum of square differences between the y values (actual binary responses) and y fitted values (the binary probabilities generated by the logistic function) represented the PSE, namely the steep

transition of the sigmoid curve.

The PSEs obtained for each trial were averaged and the baseline PSE was subtracted independently for each condition according to the formula: $PSE_{total} = (PSE_1 + PSE_2 + PSE_3)/3 - PSE_{baseline}$. Thus, PSE_{total} represents the value of how much more percentages from the face of the model were present in the morph. For instance, a PSE_{total} of 2% means that 2 more percentages of the model's face were present in the morph after the induction and, in this situation, the participant tended to identify more with the other. Reversely, a PSE_{total} of -2% means that 2 more percentages of the participant's face were present in the morph and, in this situation, the participant tended to identify less with the other.

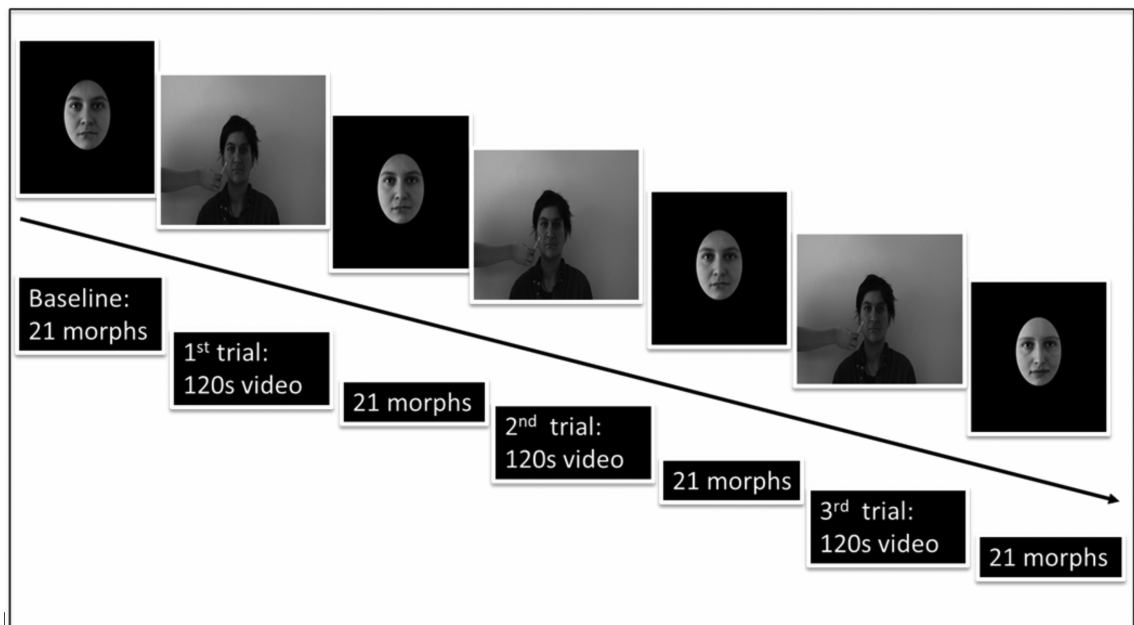


Figure 3.1: EI task: detailed representation.

After each condition, participants completed the EI questionnaire comprising 14 items divided into four subscales: ownership, appearance, disownership, and agency (Tajadura-Jimenez et al., 2011), see Appendix B.1, Table B.2 for further details. The items were measured on a 7-point Likert scale (1=strongly disagree, 7=strongly agree).

3.3.5 Data analysis

All analyses were conducted in SPSS version 25 (SPSS Inc., USA). Synchronous and asynchronous conditions for objective measures of proprioceptive drift in the RHI and PSE in

the EI were analysed using $3(\text{group}) * 2(\text{condition})$ mixed model ANOVAs. The other PD measures including proprioceptive imprecision, vision-only condition, and asynchronous random condition were analysed using between-groups one-way ANOVAs. Most variables passed Levene's test for equality of variances (the only exceptions being the vision condition in the RHI and asynchronous condition in the EI Illusion). When this assumption was violated, post-hoc t-test results of equal variances not assumed were reported (Field, 2013). When Shapiro-Wilk normality tests were violated ($p < 0.05$) (i.e. questionnaire data), non-parametric tests were run. Pearson correlations between proprioceptive imprecision and drift magnitude in each condition were also run.

Questionnaire results for both RHI and EI were analysed using non-parametric Kruskal-Wallis H tests for ordinal data comparing all groups and subsequent post-hoc non-parametric Mann-Whitney U tests comparing two independent groups.

Outliers were excluded for each condition using SPSS based on the 3rd interquartile range (IQR) (Manikandan, 2011). Thus, one outlier was excluded from the asynchronous condition, four from the vision-only condition, one from the asynchronous random condition, and three from proprioceptive imprecision. No outliers were found in the questionnaire data outside the 3-IQR. Subsequent post-hoc tests adjusted for multiple comparisons (Bonferroni corrections) assessed differences between and within groups.

The sample size was calculated using G-power calculator F-tests (Faul et al., 2007). It was based on the results obtained in the previous study in the synchronous and asynchronous conditions, setting alpha at 0.05, power at 0.8, and considering a large effect size (as indicated in Article 1), the suggested sample size was 64, thus approximately 21 participants in each group. Both control and S/L group reached this number, but the A/G group was considerably smaller (i.e. 12 participants). Previous studies using clinical population (e.g. autism) have employed samples of 12 participants (Palmer et al., 2013). Given that the S/L group was the one of interest, previously showing atypical performance on the RHI, these numbers were considered acceptable and the results replicated previous findings. Extra attention should be paid to the visual and asynchronous-random conditions and future studies should try to replicate these findings too.

3.4 Results

3.4.1 RHI proprioceptive drift results

Means and standard deviations of proprioceptive drift for each condition and in each group are shown in Table 3.1.

Table 3.1: Proprioceptive drift means \pm standard deviations in mm for each condition and in each group.

	Synchronous	Asynchronous	Visual Only	Asynchronous Random
Controls	28.83 \pm 33.04	-1.42 \pm 16.21	17.65 \pm 27.45	2.87 \pm 12.66
S/L	21.02 \pm 26.99	17.63 \pm 19.37	18.14 \pm 34.89	-3.75 \pm 13.77
A/G	10.76 \pm 20.02	0.00 \pm 19.27	18.94 \pm 15.69	4.09 \pm 18.37

A mixed model $3(\text{group}) * 2(\text{condition})$ ANOVA run on the synchronous and asynchronous conditions showed a statistically significant interaction, $F(2,54)=3.756$, $p=0.030$, $\eta^2=0.122$. There was a main effect of condition, $F(1,54)=7.918$, $p=0.007$, $\eta^2=0.128$ but the main effect of group did not reach significance $F(2,54)=2.006$, $p=0.144$, $\eta^2=0.069$. Bonferroni corrections were applied setting alpha at 0.008. An alpha value of 0.05 was divided by six comparisons (3 groups x 2 conditions) in each analysis. Post-hoc paired t-tests revealed that proprioceptive drift was significantly greater in the synchronous than in the asynchronous conditions in the control group, $t(26)=4.268$, $p < 0.001$, but not in the S/L group, $t(18)=0.453$, $p=0.656$ nor in the A/G group, $t(10)=0.888$, $p=0.395$. Independent t-tests revealed a significant higher drift in the S/L group when compared to the control group, $t(44)=-3.621$, $p=0.001$, $d=0.89$ and the A/G group, $t(29)=2.474$, $p=0.019$, $d=0.84$ for the asynchronous condition. However, this very last comparison did not survive Bonferroni corrections set as alpha = 0.008 despite having a large effect size. These results can be seen in Figure 3.2.

The other conditions were analysed using one-way ANOVAs. No significant differences were found in the vision condition between groups, $F(2,56)=0.008$, $p=0.992$, $\eta^2=0.015$ or in the random condition, $F(2,44)=1.239$, $p=0.300$, $\eta^2=0.003$. Paired t-tests re-confirmed that drift in the vision-only condition was comparable to drift in the synchronous condition in all groups: controls, $t(26)=1.772$, $p=0.088$; S/L, $t(18)=0.262$, $p=0.796$; A/G, $t(9)=-0.939$, $p=0.372$, and higher than the asynchronous condition in the

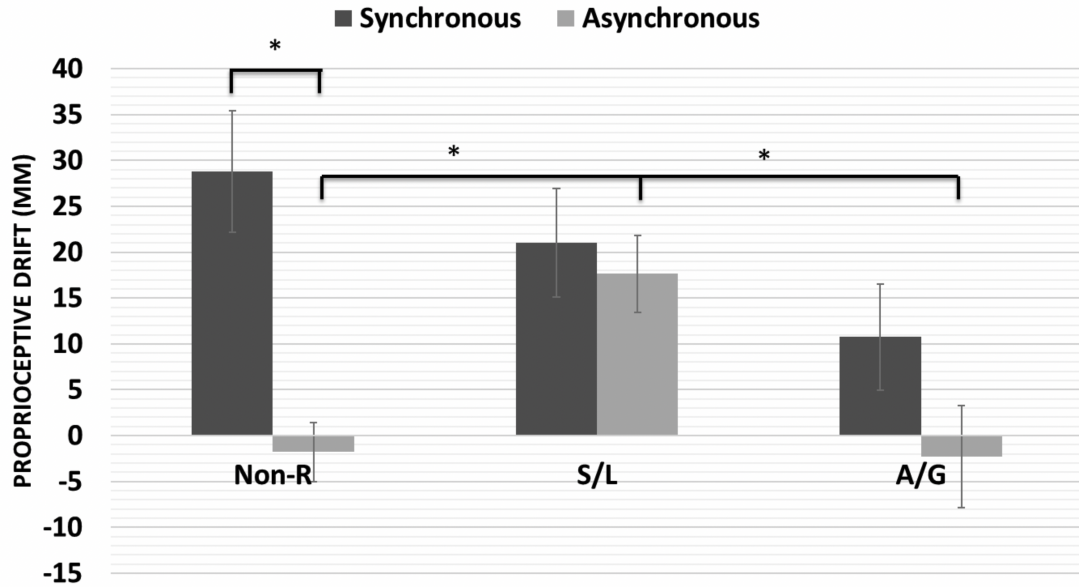


Figure 3.2: Proprioceptive drift in the synchronous and asynchronous conditions in each group. Bars indicate the mean \pm 1 standard error. Non-R= controls; S/L= sensory-localised; A/G= affective-general.

control group, $t(26)=-3.365$, $p = 0.002$ but not in the S/L group, $t(17)=-0.471$, $p = 0.643$ nor in the and A/G group, $t(10)=-1.964$, $p=0.078$. Results can be seen in Figure 3.3a. Paired t-tests showed that drift in the asynchronous random condition were lower than in the synchronous condition in controls $t(17)= 2.825$, $p = 0.012$ and the S/L group, $t(15)=3.433$, $p=0.004$, but not in the A/G group, $t(10)=0.920$, $p=0.379$. Notably, drift in the asynchronous random condition was lower than drift in the asynchronous condition in S/L group, $t(14)=3.025$, $p=0.008$, $d=0.88$ but not in controls $t(17)= -0.561$, $p = 0.582$ nor A/G group $t(10)=-0.143$, $p=0.889$. Results can be seen in Figure 3.3b.

Results obtained on the entire sample showing differences in proprioceptive drift between conditions can be seen in Appendix B.2.1. Regarding proprioceptive imprecision, there were no differences between groups $F(2,49)=2.705$, $p=0.077$, $\eta^2=0.086$. Importantly, the order of the conditions did not affect the magnitude of proprioceptive imprecision (the results can be seen in Appendix B.2.4). That is, there is no evidence that the S/L group have less reliable proprioceptive signals. However, Pearson correlations run on the entire sample showed a positive correlation between proprioceptive imprecision and drift in the asynchronous, $r = 0.301$, $p=0.036$ and vision-only, $r=0.444$, $p=0.002$ conditions. There were no correlations between proprioceptive drift and synchronous, $r=0.087$, $p=0.554$ or asynchronous random, $r=0.097$, $p=0.541$ conditions. The correla-

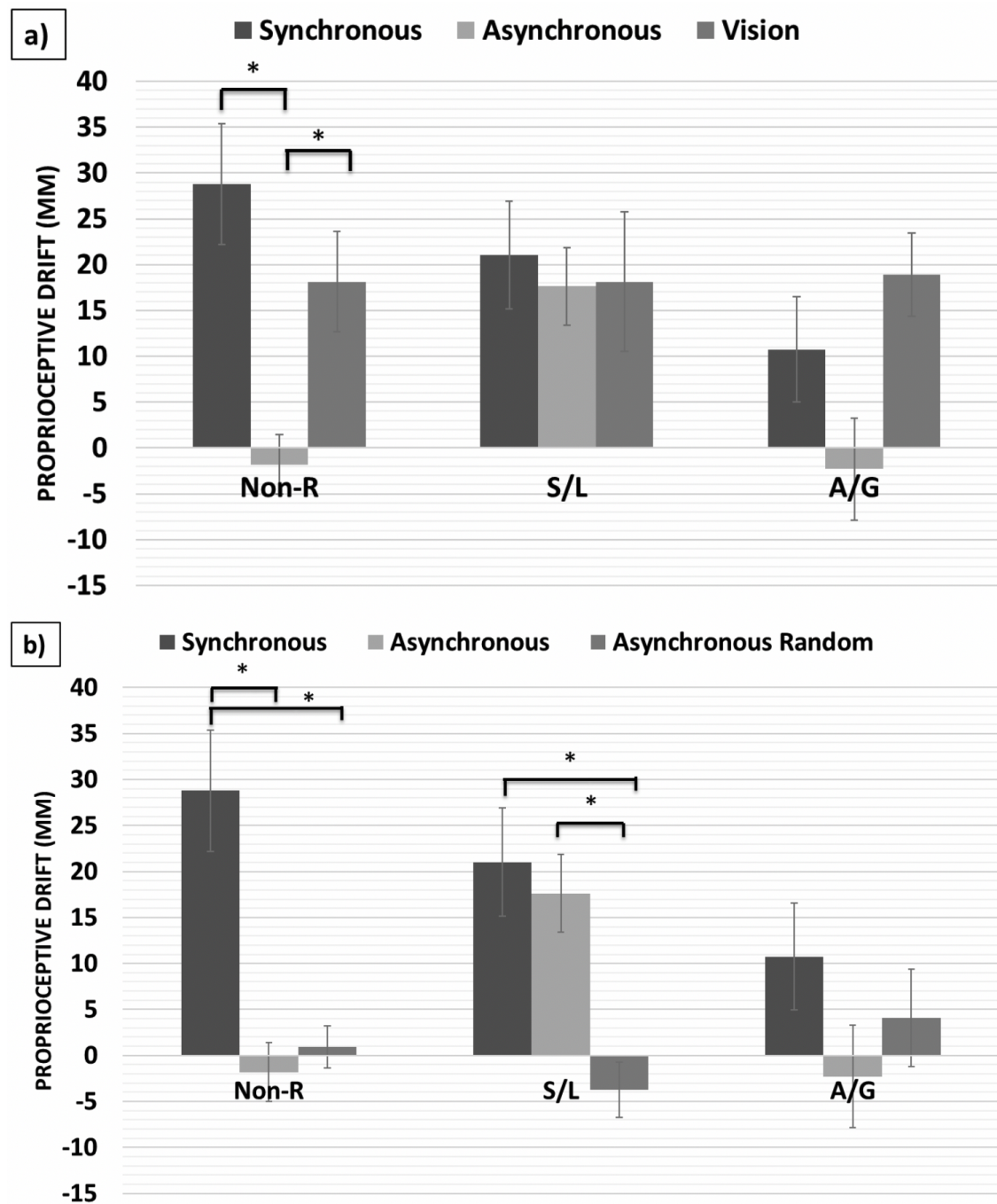


Figure 3.3: Proprioceptive drift in a) vision-only condition against synchronous and asynchronous conditions; b) asynchronous-random condition against synchronous and asynchronous conditions. Bars indicate the mean \pm 1 standard error. Non-R= controls; S/L= sensory-localised; A/G= affective-general.

tions did not reach significance in the control group for neither asynchronous: $r=0.033$, $p=0.895$, nor vision: $r=-0.102$, $p=0.686$ conditions, whilst in the A/G group the correlation was negative for the asynchronous condition: $r=-0.666$, $p=0.018$, and non-significant for the visual condition: $r=0.270$, $p=0.422$. Thus, these correlations were driven by the S/L

group where they were the strongest: for the asynchronous condition, $r = 0.716$, $p = 0.001$, for the vision-only condition, $r = 0.731$, $p = 0.001$. Correlation results can be seen in Figure 3.4.

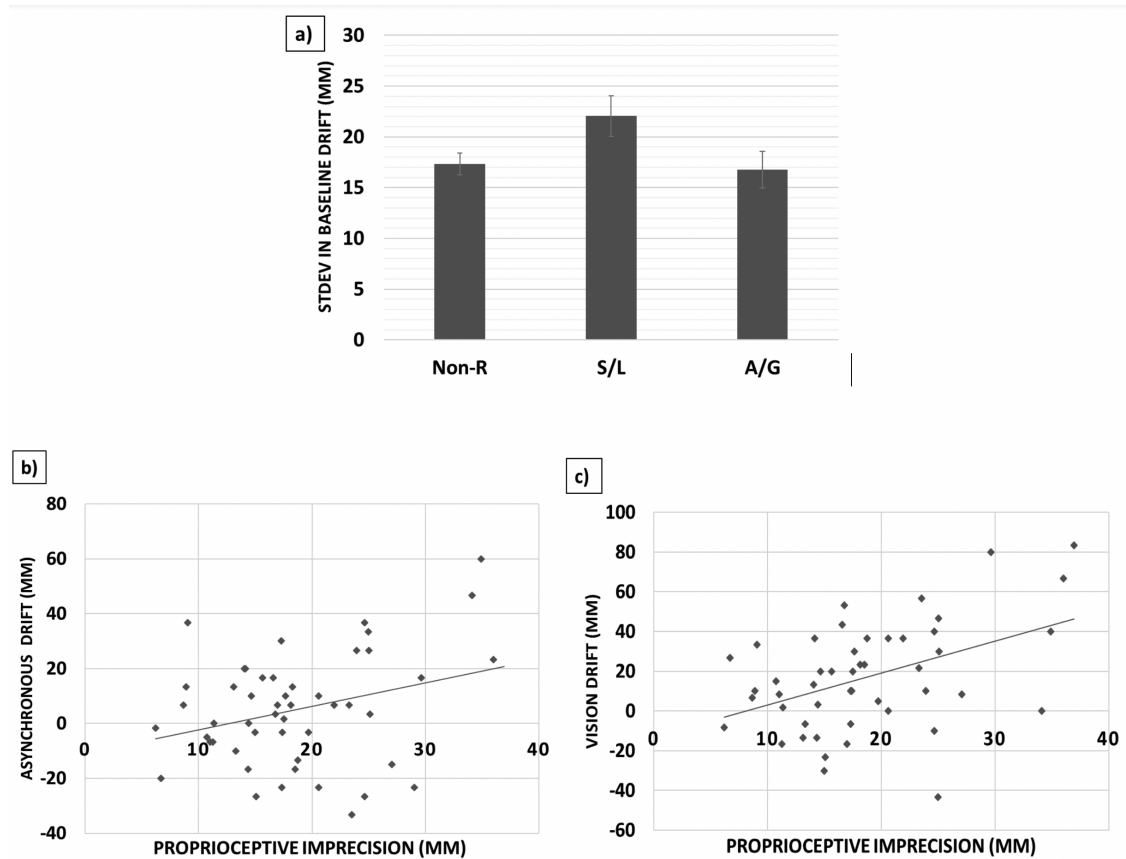


Figure 3.4: a) Proprioceptive imprecision at baseline expressed in mm; b) correlation between proprioceptive imprecision at baseline and drift in the asynchronous condition; c) correlation between proprioceptive imprecision at baseline and drift in vision-only condition.

Overall, there were no significant differences in proprioceptive drift between synchronous and asynchronous conditions in the S/L group which also recorded higher proprioceptive drift in the asynchronous condition when compared to the other two groups re-confirming that this group perceives asynchrony as synchrony. There were no significant differences between groups in the vision-only and asynchronous-random conditions between groups and drift in the asynchronous-random condition was significantly lower than drift in the asynchronous and synchronous conditions in the S/L group indicating that this group does not rely more on visual capture and that disrupting tactile-temporal expectations inhibits susceptibility to the illusion in this group. There are no differences in proprioceptive imprecision between groups but there is a correlation between proprioceptive imprecision and the magnitude of proprioceptive drift in

asynchronous and vision conditions driven by the S/L group suggesting that S/L do not have higher proprioceptive imprecision, but they are more susceptible to it.

3.4.2 RHI Subjective ratings

The medians of RHI subjective ratings for each condition and in each group can be seen in Table 3.2.

Table 3.2: Medians for each condition and each subscale of the RHI questionnaire.

	Synchronous			Asynchornous			Visual-only			Asynchronous Random		
	Own	Loc	Age	Own	Loc	Age	Own	Loc	Age	Own	Loc	Age
Non-resp	5.00	4.33	4.00	1.80	2.00	1.50	2.4	2.67	1.00	2.20	2.33	1.00
S/L	5.20	4.50	4.50	2.20	2.67	2.00	2.50	2.67	1.25	2.89	2.89	2.64
A/G	5.00	4.33	4.00	2.20	2.67	2.00	2.40	2.67	1.00	2.40	2.33	2.00

Non-parametric Kruskal-Wallis H tests for ordinal data were used to analyse differences between groups for each condition and on each of the subscales. There were no significant differences between groups on any of the conditions or subscales. The results of Kruskal-Wallis H tests can be seen in Table 3.3.

Table 3.3: Kruskal-Wallis H test results indicating differences between groups for each condition and subscale.

	Ownership	Location	Agency
Synchronous	H= 0.770	H= 0.050	H= 0.802
	p= 0.681	p= 0.975	p= 0.670
Asynchronous	H= 2.238	H= 4.125	H= 3.657
	p= 0.372	p= 0.127	p= 0.161
Vision-only	H= 0.287	H= 0.752	H= 0.166
	p= 0.866	p= 0.687	p= 0.920
Asynchronous-Random	H= 0.905	H= 1.724	H= 4.330
	p= 0.920	p= 0.422	p= 0.115

Results obtained on the entire sample showing difference in subjective ratings between conditions can be seen in Appendix B.2.2. Overall, these results indicate that there were no differences between groups on any of the subjective report measures, re-confirming the drift results obtained in the synchronous, vision-only and asynchronous-random conditions but not in the asynchronous condition.

3.4.3 EI: Point of Subjective Equality (PSE) results

PSE means and standard deviations expressed as percentages for each condition and in each group are shown in Table 3.4.

Table 3.4: Means \pm standard deviations expressed in percentages of the difference between post-induction PSE and baseline PSE for each condition and in each group.

	Synchronous	Asynchronous
Controls	5.93 \pm 4.76	2.72 \pm 4.92
S/L	5.07 \pm 6.84	5.11 \pm 3.45
A/G	4.50 \pm 4.67	-0.50 \pm 2.13

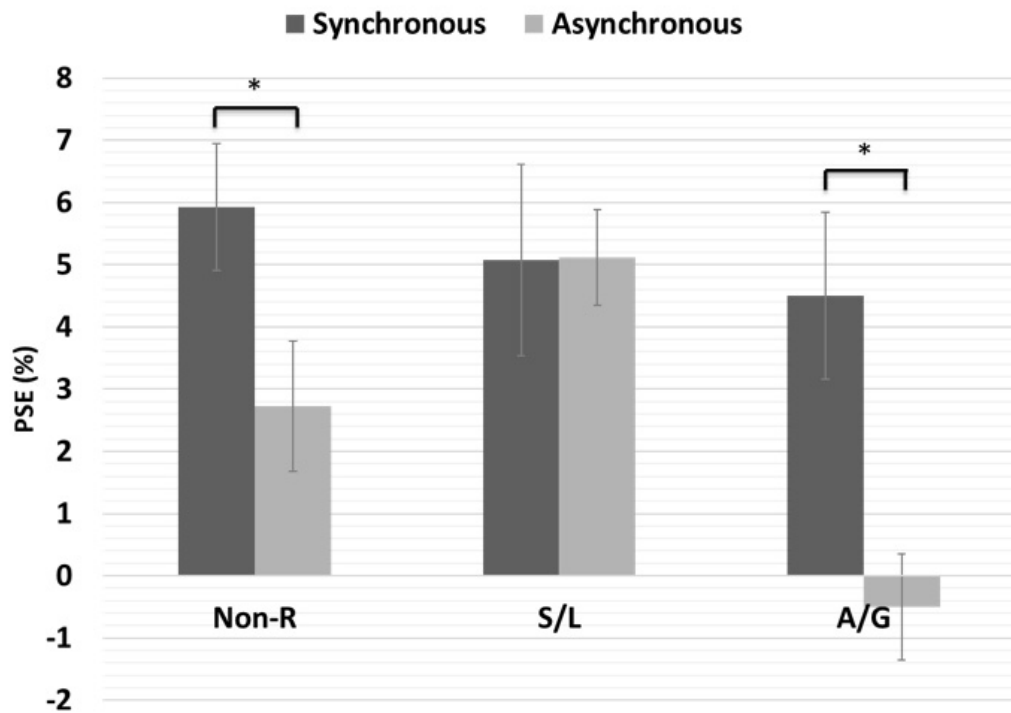


Figure 3.5: PSE for synchronous and asynchronous conditions in each group. Bars indicate the mean \pm 1 standard error. Non-R= controls; S/L= sensory-localised; A/G=affective-general.

PSE for the synchronous and asynchronous blocks were analysed in a mixed model $3(\text{group}) * 2(\text{condition})$ ANOVA. The results showed a statistically significant interaction, $F(2,50)=3.418$, $p=0.041$, $\eta^2=0.120$. There was a main effect of condition, $F(1,50)=12.363$, $p=0.001$, $\eta^2=0.198$ but the main effect of group did not reach significance $F(2,50)=2.271$, $p=0.114$, $\eta^2=0.083$. Post-hoc paired t-tests revealed that the point of subjective equality

(PSE) was significantly greater in the synchronous than in the asynchronous conditions in the control group, $t(22)=3.850$, $p = 0.001$, and in the A/G group, $t(11)=3.561$, $p = 0.004$, but not in the S/L group, $t(17)=-0.022$, $p=0.983$. Independent t-tests revealed a significant higher PSE in the S/L group when compared to the A/G group, $t(28) = -5.024$, $p=0.001$, $d = 1.38$ but not the control group $t(39) = -1.749$, $p = 0.088$, $d=0.53$ for the asynchronous condition. These results can be seen in Figure 3.5.

3.4.4 EI: Subjective ratings

Medians of EI subjective ratings for each condition and in each group can be seen in Table 3.5.

Table 3.5: Medians in EI subjective ratings in each group and for each condition and subscale.

	Synchronous				Asynchronous			
	Ownership	Appearance	Agency	Disownership	Ownership	Appearance	Agency	Disownership
Non-resp	2.20	4.33	2.50	3.00	1.40	2.67	2.00	2.00
S/L	2.90	4.83	4.50	4.00	2.50	5.50	2.75	3.50
A/G	2.80	5.00	2.75	3.50	1.40	3.00	1.75	3.00

Non-parametric Kruskal-Wallis H tests for ordinal data were used to analyse differences between groups for each condition and on each of the subscales. There were no significant differences between groups on most of the conditions or subscales except for the disownership subscale in the asynchronous condition as it can be seen in Table 3.6. Further Mann-Whitney U test revealed that the S/L group reported greater disownership in the asynchronous condition than the control group $Z = -2.634$, $p = 0.008$, $d = 0.81$.

Table 3.6: Kruskal-Wallis H test results indicating group differences in EI subjective ratings for each condition and each subscale.

	Ownership	Appearance	Agency	Disownership
Synchronous	H= 1.279 p= 0.528	H= 1.953 p= 0.377	H= 5.613 p= 0.060	H= 3.956 p= 0.174
Asynchronous	H= 3.495 p= 0.174	H= 3.336 p= 0.189	H= 1.974 p= 0.373	H= 7.040 p= 0.030

3.5 Discussion

The present study further explored bodily ownership in vicarious pain responders by interpreting the atypical susceptibility to the RHI observed in sensory-localised vicarious pain responders through the Bayesian sensory inference model (Samad et al., 2015) and by exploring their performance on a second bodily ownership paradigm, namely the EI. Our results for both RHI and EI paradigms indicated no significant difference between synchronous and asynchronous conditions in the S/L group, reconfirming previous results showing that S/L responders perceive asynchrony as synchrony.

The EI and RHI present numerous similarities and, together with full body ownership illusions, they exploit the same mechanisms of multisensory integration, all these illusions being stronger when there is a perfect match between the incoming sensory signals (Serino et al., 2013). Furthermore, both EI and RHI tap on similar mechanisms of bodily-ownership and, during the experience of embodying a different body part, be it a hand or a face, same multimodal parietal brain regions are recruited including the intraparietal sulcus (IPS) and the temporo-parietal junction, and the premotor cortex, an area with high density of mirror-neurons (agency/correspondence of actions give the illusion of ownership) (Ehrsson et al., 2004; Tsakiris et al., 2006; Apps et al., 2013). The difference between the RHI and the EI consists in the fact that the latter taps into mnemonic processes of recognition and facial identity besides the ones of bodily ownership. This is supported by neuroanatomical evidence indicating the recruitment of areas processing facial identity in the EI, mainly the unimodal inferior occipital gyrus, a crucial component in the face perception network that responds to synchronicity and enhanced feeling of ownership (Nagy et al., 2012).

Considering the above, our results suggest that bodily perception and recognition mechanisms differ in S/L responders. These mechanisms rely on multisensory integration processes and lead to a greater tendency to alter self-other bodily representations. Mainly, S/L responders seem to rely more on tactile and corporeal priors as further discussed.

3.5.1 RHI results and the Bayesian Sensory Inference Model

Firstly, our results indicated no significant difference between proprioceptive drift in the synchronous and asynchronous conditions in the S/L group. There were also no significant differences between these two conditions in A/G responders, but the sample was small, and these results were due to a low drift in the synchronous condition in this group and not to a higher drift in the asynchronous one. These results may suggest that the A/G group is less susceptible to the illusion, however, after collapsing drift results from first and second study and obtaining a very robust sample, there were no significant differences between this group and controls as it can be seen in Appendix B.3.

We did not obtain significant differences in the questionnaire data, but the sample was considerably smaller than in the previous experiment. Furthermore, it has been previously indicated that the reported subjective experience of the illusion and the perceived location of the hand as measured by drift magnitude may be correlated (Tsakiris and Haggard, 2005) but they do not necessarily correspond to each other (Rohde et al., 2011; Holle et al., 2011; Carruthers, 2013; Riemer et al., 2015). In our sample, the drift correlated with the subjective ratings only for the asynchronous and vision conditions as it can be seen in Appendix B.2.3. Drift and subjective ratings are believed to correspond to two different dimensions of bodily ownership: body-location (i.e. proprioceptive drift) and body-ownership (i.e. subjective experience of ownership and/or agency) (for a review see Serino et al. (2013)) and they also have different neuronal correlates: rTPJ is involved mainly in self-location and vPMc/PPc in body ownership.

Regarding the other two conditions that were introduced in this study, there were no significant differences between groups in the vision-only condition nor in the asynchronous-random condition. According to the Bayesian sensory inference model, the illusion depends on the match and strength of the incoming sensory signals and high precision signals, such as vision, outweigh less precise signals such as proprioceptive location. The vision-only condition was used in order to establish if the S/L group relies more on visual input, leading to a biased estimation of hand location based on the place where the vision signal comes from (i.e. the place of the dummy hand). The clear absence of significant differences between this group and the other two groups indicates that they do not rely more on visual capture. Importantly, the overall results matched the predictions

of the model, namely that the illusion occurs in the vision-only condition. Our results indicated comparable drift in the vision-only condition with the one in the synchronous condition in line with previous results obtained by Rohde et al. (2011) and Samad et al. (2015). Also, drift in the vision only condition was higher than in the asynchronous condition in the control group but not in the S/L group indicating that the S/L group has a similar performance on all these conditions. The questionnaire results indicated that the subjective experience of the illusion is still stronger in the synchronous condition than in the vision-only condition suggesting that the synchronous condition indeed provides the strongest evidence for the illusion as previously vehiculated. It also re-enforces the fact that subjective perception and objective drift are two different dimensions of the illusion.

The asynchronous-random condition was introduced in order to test the hypothesis that S/L responders rely more on tactile-temporal predictions. The Bayesian sensory model uses causal inference to predict optimal estimates of location and time which are subsequently matched to the actual incoming sensory signals. Thus, a match between expectations and input signals would result in a greater likelihood of attributing a common cause, as it usually happens in the synchronous condition but not in the asynchronous condition when there is a temporal delay. Importantly, high correlation between multi-sensory events can lead to the attribution of a common cause (Parise et al., 2012) and this may happen in the asynchronous condition due to the perfect correlation of visual and tactile signals. This may also explain why sometimes a small positive drift is observed in the general population in the asynchronous condition but significantly smaller than synchronous drift (Botvinick and Cohen, 1998; Tsakiris and Haggard, 2005). In the asynchronous-random condition, the tactile-temporal rhythmicity of the asynchronous condition was disrupted so participants could not predict the time of the next stroke. Thus, we would expect asynchronous random drift to be smaller than the asynchronous drift and the illusion completely suppressed. In the entire sample, the drift was smaller in asynchronous-random compared to the asynchronous condition and very close to 0 (see Appendix B.2.1) suggesting that this condition severely disrupts the illusion. In the S/L group, asynchronous random drift was negative and significantly smaller than drift in the asynchronous condition indicating that this group strongly relies on tactile-temporal expectations and that the high correlation between tactile and temporal signals

is critical for in this group for experiencing the illusion.

Results in proprioceptive imprecision showed no differences between groups suggesting that the S/L group does not have higher tactile imprecision which would be easily overwritten by visual input and lead to higher drift in conditions other than the synchronous one. However, there was a positive correlation between proprioceptive imprecision and drift amplitude in asynchronous and visual conditions. Importantly, this correlation was led by the S/L group indicating that, if proprioceptive imprecision is higher in S/L responders, they are more likely to report a higher drift in synchronous and asynchronous conditions and are more susceptible to proprioceptive imprecision compared to the other two groups. Interestingly, the correlation was observed only for the asynchronous and vision-only conditions which may be in line with previous predictions of the Bayesian sensory inference model, namely that the synchronous condition generates the highest drift, being the condition of maximum saturation and that the asynchronous random condition would completely abolish drift being at the other end of the spectrum.

Altogether, the results obtained suggest that vision is not a stronger signal and that proprioceptive imprecision is not weaker in the S/L group. However, S/L responders rely more on tactile-temporal correlations recalibrating visual and tactile modalities and attributing a common cause to them and they are also more susceptible to proprioceptive imprecision.

3.5.2 EI results

The point of subjective equality (PSE) was comparable in the synchronous and asynchronous conditions in the S/L group indicating that S/L responders identify more with the other's face in both conditions and re-confirming that asynchrony is perceived as synchrony in this group. Considering previous results obtained in the RHI, we can assume that this is due to the perfect tactile-temporal correlation. Moreover, the EI does not have a proprioceptive component so the results obtained can be mainly attributed to tactile-temporal rhythmicity and meeting strong tactile expectations (i.e. receiving the stroke when it is expected).

The subjective ratings results registered higher disownership over own's face in the

S/L group when compared to controls in the asynchronous condition, but no differences were recorded in the other three subscales including ownership, appearance, and agency. This may indicate a propensity in this group towards disowning self in order to identify or feel the other, or just a higher tendency towards depersonalisation traits or depersonalisation-like experiences (Bowling et al., 2019). In this task, objective and subjective measures of the illusion seem to be more in line with each other, however, there are not in perfect agreement. PSE, analogously to proprioceptive drift, is an objective measure of self-other facial identity which is obtained after participants decide if the morphs that they see look more like themselves or like the model. This decision is not informed by the awareness of the direction of their choice (i.e. if they decided that the morphs look more or less like themselves). When filling out the questionnaire, participants have full awareness of the perceived identity with the other. Thus, these objective and subjective measures may tap on different mechanisms of bodily awareness and the questionnaire measure may require a stronger experience.

Overall, both EI and RHI seems to occur in a similar fashion in S/L vicarious pain responders as it has been previously recorded in MTS participants who experience both illusions in a touch-only condition (Davies and White, 2013; Maister et al., 2013). We do not know how S/L responders would perform in different conditions such as vision-only or touch only conditions in the EI. However, we would expect to notice a positive effect in PSE the vision-only condition, only by looking at a face being stroked, with the synchronous condition still providing the strongest evidence for the illusion, as previously recorded by Maister et al. (2013) and to register a comparable PSE amongst all three groups in these two conditions, analogously to the drift results obtained in the RHI task. We would not expect a significant positive change in PSE in the touch-only condition since S/L responders do not necessarily feel touch when seeing someone being touched, despite the fact that a small subgroup may display MTS like traits (Ward et al., 2018). Thus, a touch-only condition would be the equivalent of a synchronous condition (feeling touch when seeing touch) in MTS but not in S/L responders. Theoretically, the occurrence of the EI can be attributed to multisensory integration in a Bayesian sensory inference fashion, in which visual and tactile modalities would operate generating temporal and spatial signals attributed to a common cause. However, more empirical research is needed in order to test this model in EI and to record performance on various

conditions for a better understanding of underlying mechanisms in EI.

3.5.3 General Conclusions

The present study further explored susceptibility of vicarious pain responders to bodily ownership illusions by employing both RHI and EI paradigms.

The Bayesian sensory inference model was successfully applied to the RHI paradigm and the model's general predictions were all met as shown by analyses conducted on the entire sample. The confirmed predictions included: a) the higher precision of the visual modality; b) positive correlation between drift magnitude and the degree of proprioceptive imprecision; c) illusion was severely disrupted when tactile-temporal correlations were completely violated.

Regarding vicarious pain responders, our results mainly indicated that S/L responders display atypical susceptibility to bodily ownership illusions perceiving asynchrony as synchrony. This unusual pattern is due to differences in prior probabilities and in the ability to re-calibrate visual and tactile modalities and to generate the experience based on their perfect correlation.

Article III: Individual Differences in Vicarious Pain Perception Linked to Heightened Socially Elicited Emotional States

4.1 Abstract

For some people (vicarious pain responders), seeing others in pain is experienced as pain felt on their own body and this has been linked to differences in the neurocognitive mechanisms that support empathy. Given that empathy is not a unitary construct, the aim of this study was to establish which empathic traits are more pronounced in vicarious pain responders. The Vicarious Pain Questionnaire (VPQ) was used to divide participants into three groups: (1) non-responders (people who report no pain when seeing someone else experiencing physical pain), (2) sensory-localised responders (report sensory qualities and a localised feeling of pain) and (3) affective-general responders (report a generalized and emotional feeling of pain). Participants completed a series of questionnaires including the Interpersonal Reactivity Index (IRI), the Empathy Quotient (EQ), the Helping Attitudes Scale (HAS), and the Emotional Contagion Scale (ECS) as well as The Individualism – Collectivism Interpersonal Assessment Inventory (ICIAI) and a self-other association task. Both groups of vicarious pain responders showed significantly greater emotional contagion and reactivity, but there was no evidence for differences in other empathic traits or self-other associations. Subsequently, the variables were grouped by a factor analysis and three main latent variables

were identified. Vicarious pain responders showed greater socially elicited emotional states which included the ECS, the Emotional Reactivity Subscale of EQ and the HAS. These results show that consciously feeling the physical pain of another is mainly linked to heightened emotional contagion and reactivity which together with the HAS loaded on the socially elicited emotional states factor indicating that, in our population, these differences lead to a more helpful rather than avoidant behaviour.

4.2 Introduction

Some people automatically experience and re-create the physical pain of others on their own body and this has been known as vicarious pain responses or synaesthesia for pain (Fitzgibbon et al., 2010b). Vicarious pain responses are mainly attributed to shared representations of self and other and supported by overlapping neuronal mechanisms of self-other pain processing (Lamm et al., 2011). Moreover, specific functional and structural neuronal patterns have been distinguished in populations characterized by conscious vicarious pain responses (Grice-Jackson et al., 2017a).

In our past work, we developed the vicarious pain questionnaire (VPQ) (Grice-Jackson et al., 2017a) which separates participants into three categories when they observe the physical pain of others: 1) non-responders (report no pain when watching a video with someone else experiencing physical pain), 2) sensory-localised responders (report a localised feeling of pain in the same location as the person in the video), and 3) general-affective responders (report a generalized and emotional feeling of pain). The last two categories have been previously referred to as pain-responders (Osborn and Derbyshire, 2010). Moreover, the sensory-localised group displays a capacity of mirroring the pain of another on oneself in a fashion similar to the tactile mirroring encountered in mirror-touch synaesthetes (Ward and Banissy, 2015). In the present study, we further investigate how individual differences in vicarious pain perception are linked to both affective and cognitive empathic traits.

A common link has been drawn in the literature between simulating the pain of others and empathy – the capacity to share and understand the emotional states of the others (De Vignemont and Singer, 2006; Lockwood, 2016). Importantly, empathy is not a unitary construct; it implies various components including affective empathy such as emotional contagion or emotional reactivity, cognitive empathy also referred to as theory of mind (ToM) or perspective taking, and compassionate empathy or empathic concern which can be associated with the action to help and alleviate other's suffering (Bernhardt and Singer, 2012). Vicarious pain responses seem to have both a strong affective empathic component since they involve the representation of the painful emotional state of the other but also a cognitive/compassionate component. It is not clear yet to which extent feeling the physical pain of another benefits or impairs social interactions

since the affective aspect of empathy is a fundamental process that allows recognizing and simulating others' emotional states, but it does not necessarily require a cognitive understanding of their states (Bird and Viding, 2014). Vicarious pain responses seem to be mainly associated with an emotional reaction toward others' states and previous research has indicated that individuals reporting conscious vicarious sensations, such as mirror touch synaesthetes (MTS), are more likely to score higher on the emotional reactivity subscale of the empathy quotient (EQ) but not on the other subscales (social skills and cognitive empathy) (Banissy and Ward, 2007). In this study, we use both the emotional reactivity subscale of the EQ and, for the first time, the emotional contagion questionnaire to further investigate their association with vicarious pain responses.

There is still a debate regarding the extent to which emotional contagion and reactivity are related to empathy *per se*. For instance, Bird and Viding (2014) highlight that emotional contagion is a precursor of empathy and not an intrinsic component since empathy needs a clear distinction between self and other to occur. Moreover, a complete overlap between self and other representations would produce distress and impair the ability to switch between self and other perspectives (Lockwood, 2016). Thus, it is not clear whether strong emotional reactivity, as previously witnessed in vicarious perception, leads to empathic concern and altruistic behaviour or, on the other hand, to personal distress and socially avoidant behaviours. It has been reported that higher levels of affective empathy lead to altruistic/prosocial behaviour (Batson et al., 1981, 1997) and that pain intensity ratings correlate with higher empathic traits (Lamm et al., 2007). However, higher levels of personal distress can also be triggered when witnessing other's pain, especially if this is accompanied by a negative outcome (Lamm et al., 2007). As such, there is likely to be a fine balance between the extent to which one can tune into the feelings of others, and also the extent to which one can tune out (using emotional regulation) to guard against personal distress.

Previous research has shown that self-other control (the ability to switch focus on information relevant to oneself or relevant to another person) improves performance in social cognitive domains. For instance, increased motor self-other control results in an increased vicarious pain perception (as measured by corticospinal activity and subjective ratings) and self-reported empathy in typical adults (de Guzman et al., 2016). This is in line with theoretical models of empathy suggesting that interactions between self-other

control and vicarious perception may explain individual differences in empathy (Bird and Viding, 2014), which could perhaps be extended to those studied here. To date, few studies have studied self-other mechanisms in conscious vicarious pain responders (e.g. Derbyshire et al. (2013)). Addressing this gap can enable a greater understanding of the structure of empathy (e.g. Bird and Viding (2014); Ward and Banissy (2015)), including how individual differences in pain perception affect social cognition (e.g. Happé et al. (2017)).

To identify which empathic traits vary in vicarious pain responders, we used a series of questionnaires looking at all these dimensions in the three different groups of people, recruited from the neurotypical population, but classified according to the VPQ. The groups represented the independent variable. The dependent measures were: emotional contagion scale (ECS), the helping attitudes scale (HAS), the interpersonal reactivity index (IRI), and the empathy quotient (EQ). These measures were employed to touch on all aspects of empathy from basic emotional contagion to motivational/compassionate empathy, including cognitive and affective aspects of empathy. Notably, most people do not manifest their compassion equally and they tend to favor those who are close to them (e.g., family, partners) and their ingroups over strangers and/or out-groups. This also applies to measures relating to vicarious pain (Avenanti et al., 2010; Hein et al., 2010) and suggests a form of control mechanism by which people gate their empathic responses according to the degree to which others are self-related. For instance, family closeness is the strongest followed by closeness towards friends, colleagues and finally strangers (Matsumoto et al., 1997). As such, we tested whether vicarious pain responders show a different pattern (e.g. treating strangers like family) that might give rise to a different empathic response. We investigated the possible differences in the degree of social closeness and self-saliency in vicarious pain responders using the individualism-collectivism attitudes questionnaire (Matsumoto et al., 1997) and an abstract self-other association task (Sui et al., 2012). Sui et al. (2012) showed how people have faster reaction times when responding to an association made between self and an abstract shape than between another person (friend or stranger) and an abstract shape. These results support the idea that the self is prioritised, and this also seems to vary with cultural differences (Sui et al., 2012). Since vicarious pain responders attribute other's sensations to the self (they perceive the other's physical pain as their own), we may hypothesise that

they have a higher ability to prioritise other's sensations over the self thus overcoming the egocentricity bias, where self-sensations tend to be prioritised over other-sensations (see (Silani et al., 2013)). The same tendency could be manifested at a higher cognitive level through top-down mechanisms which would actively switch from self to other's saliency (Bird and Viding, 2014). As such, we would expect the self not to be as prioritised in vicarious pain responders and a linear trend in reaction times showing that this population treats unknown others as close ones or as self. We would expect the self not to be as prioritised in vicarious pain responders and a linear trend in reaction times showing that this population treats unknown others as close ones or as self.

4.3 Materials and methods

4.3.1 Participants

A total of 125 participants (mean age = 20.89, SD = 3.34; 104 females) completed the study. Participants were recruited via email invitation or via SONA from Sussex University and Goldsmiths, University of London. Each participant had previously completed the VPQ online via Bristol Online Survey (BOS) and were divided into three groups: controls (C), sensory-localised (S/L) and affective-general (A/G). The three groups were derived from a cluster analysis of a much larger dataset of participants who have completed the VPQ (Aged 18–60 years, $M = 20.42 \pm 4.16SD$, 297 Males, 759 Females). Overall, there were 68 participants classed as controls, i.e., non- responders (mean age = 20.37, SD = 3.26, 58 females), 37 participants classed as S/L responders (mean age = 21.81, SD = 3.67, 29 females) and 21 participants classed as A/G responders (mean age = 21.00, SD = 2.76, 17 females). The groups did not differ by age [$F(2, 124) = 2.241, p = 0.111, \eta^2 = 0.035$] or gender ($\chi^2 = 0.469, p = 0.791$). All participants completed the questionnaires: EC, EQ, IRI, HAS, and ICIAI (controls: N = 68 S/L: N = 37, A/G: N = 21). Due to technical issues, not all participants completed the *self- other association task* (controls: N = 55, S/L: N = 25, A/G: N = 16). Ethical approval was obtained from the Science and Technology Research Ethics Committee of the University of Sussex and all participants offered their written informed consent at the beginning of the study using an online form.

The sample size was calculated for the self-other association task a-priori, setting

alpha at 0.5, power at 0.8 and the effect size at 0.48 based on the self-saliency effect size indicated by Sui et al. (2013a) resulting in a sample of 75 participants (i.e. 25 participants in each group). Observed power analyses were run a-posteriori for questionnaire data. These were relatively small for individual subscales with the exception of the empathy quotient and the emotional contagion scales which had an observed power of 0.8 and 0.7 respectively. The other questionnaire measures had observed power varying between 0.3 and 0.6. Collapsing the various measure onto three factors after running the factor analysis, considerably increased the power of the study. Thus, the observed power for socially elicited emotional states and low emotion regulation being 0.89 and 0.71 respectively.

4.3.2 Measures

Vicarious Pain Questionnaire

The VPQ is comprised of 16 videos (no audio) of people experiencing physical pain (e.g., falls, sports injuries, injections), each video lasting for approximately 10 s (Grice-Jackson et al., 2017). After each video, participants were questioned about their experience. First, participants were asked if they experienced a bodily sensation of pain while viewing the video (yes/no). If the answer was 'yes,' participants were asked to describe their pain by answering three more questions about their experience: (1) how intense their pain experience was (1–10 Likert scale, 1 = very mild pain, 10 = highly intense pain); (2) if and where they localised the pain, answering options were either 'localised to the same point as the observed pain in the video,' 'localised but not to the same point,' and 'a general/non-localisable experience of pain'; (3) to select pain adjectives from a list that best described their vicarious pain experience (10 sensory descriptors such as 'tingling,' 'burning,' 'stinging,' 10 affective descriptors such as 'nauseating,' 'grueling,' 'aversive' and three cognitive-evaluative descriptors 'brief,' 'rhythmic,' 'constant'). All these answers were used to generate the three variables that were entered the two-step cluster analysis (i.e., pain intensity, localised-generalized responses, and sensory – affective responses) which subsequently generated the three groups (for further details see (Botan et al., 2018b)).

Emotional Contagion Scale

The ECS (Doherty, 1997) is a 15-item self-reported unidimensional scale, with high reliability (Cronbach's $\alpha = 0.90$) which assesses the susceptibility to others' emotions. The ECS consists of five basic emotions: love, happiness, sadness, anger, and fear. Each emotion is represented by three items (e.g., *'If someone I'm talking with begins to cry, I get teary-eyed'* or *'Being with a happy person picks me up when I'm feeling down'*) that are scored on a 5-point Likert scales from 1 – *not at all* to 5 – *always*, with a higher score indicating higher emotional contagion.

Empathy Quotient

A short 15-item version of the EQ (Muncer and Ling, 2006) was used comprising five items for each of the three subscales: Social Skills (SS) (e.g., *'I find it hard to know what to do in a social situation'*) (Cronbach's $\alpha = 0.57$), Cognitive Empathy (CE) (e.g., *'I am good at predicting how someone will feel'*) (Cronbach's $\alpha = 0.74$), and Emotional Reactivity (ER) (e.g., *'Seeing people cry does not really affect me'*) (Cronbach's $\alpha = 0.63$). Participants gave their responses on a 4-point Likert scale, ranging from 1 – *strongly disagree* to 4 – *strongly agree*.

Interpersonal Reactivity Index

The Interpersonal Reactivity Index, or IRI (Davis, 1983), is a multidimensional scale, comprised of 28 items divided into four subscales. The subscales are Perspective Taking (PT) (e.g., *'I try to look at everybody's side of a disagreement before I make a decision'*), Fantasy Scale (FS) (e.g., *'After seeing a play or movie, I have felt as though I were one of the characters.'*), Empathic Concern (EC) (e.g., *'I am often quite touched by things that I see happen.'*), and Personal Distress (PD) (e.g., *'When I see someone who badly needs help in an emergency, I go to pieces'*). Each subscale consists of seven items and responses are given on a fivepoint scale 0 – *does not describe me very well* to 4 – *describes me very well*.

Helping Attitudes Scale

The Helping Attitude Scale (Nickell, 1998) is a self-report unidimensional measure of pro-social and helping tendencies with good internal consistency (Cronbach's $\alpha = 0.869$). It comprises 20 items scored on a 5-point Likert scale (1 = *strongly disagree* to 5 = *strongly agree*). Examples of items are: '*Helping others is usually a waste of time*'; '*When given the opportunity, I enjoy aiding others who are in need*'; '*It feels wonderful to assist others in need*'.

The Individualism – Collectivism Interpersonal Assessment Inventory (ICIAI)

The Individualism – Collectivism Interpersonal Assessment Inventory (ICIAI) (Matsumoto et al., 1997) assesses values (Part 1) and behaviours (Part 2) when interacting with others. It takes into account the degree of closeness with the other in four relationship groups: family, friends, colleagues and strangers. We were mainly interested in behaviours and so we only used the second part of the questionnaire. Participants scored from 0 = *never* to 6 = *all the time* how much they engaged in each of the mentioned behaviours in each of the four relationship groups. The reliability of the questionnaire is high with Cronbach's $\alpha = 0.90$. The questionnaire contains 19 items and examples are: '*Maintain self-control towards them*'; '*Share blame for their failures*'; '*Sacrifice your possessions for them*'; '*Respect them*' etc.

Self-Other Association Task

The self-other association task (Sui et al., 2012) requires participants to respond to an association between a geometric shape (triangle, square, or circle) and a label (self, a named best friend, or an unfamiliar person). Participants were first asked to name a best friend and the time period they had known each other for. Then each of the three geometrical shapes was randomly associated to a label (e.g., *you are a circle, the stated friend is a triangle, and a stranger is a square*). In the matching phase, the participants had to judge if the match shapes- label pairings was correct. A pairing of a shape and a label (e.g., \triangle – *stranger*) was presented for 500 ms. The pairing was generated at random and it could conform to the initial instruction which associated each shape to a specific label, or it

could be a recombination of a label with a different shape. Immediately after, participants were expected to judge if the association was correct or not. Participants first performed a practice phase containing 20 trials when they were given written feedback (correct or incorrect) followed by three blocks of 120 trials. Thus, there were 60 trials in each condition across all blocks (self-matched, self-nonmatched, familiar-matched, familiar-nonmatched, unfamiliar-matched, and unfamiliar-nonmatched). Reaction times were recorded and analysed as dependent variable in a mixed model ANOVA.

4.3.3 Procedure

The questionnaires were administered via Bristol Online Survey (BOS), an online software for collecting questionnaire data. The self-other association task was run via Inquisit¹, an online survey for collecting both questionnaire and tasks data. Participants filled in the questionnaires and, subsequently, they were redirected to the task. The study took approximately 40 min (30 min for questionnaires and 10 min for the task). All questionnaires were completed in the same order (as outlined above), so groups were matched in this regard.

4.3.4 Statistical Analyses

Analyses of variance (one-way ANOVAs) were used to establish differences between groups on each questionnaire. Mixed models analyses of variance were run on the ICIAI (3 groups * 4 conditions ANOVAs) and on the self-other association tasks (3 groups * 3 conditions ANOVAs). Variables were treated as continuous and the great majority of them were normally distributed as shown by Shapiro–Wilk tests and histograms. Normality assumptions were violated only in the following cases: controls [IRI-EC ($p = 0.01$) and ICIAI family ($p = 0.01$) and colleagues ($p = 0.04$)]; S/L [EQ-CE ($p = 0.02$), IRI-EC ($p = 0.01$)]. For these cases, Kruskal–Wallis non-parametric tests were run, re-confirming the results (see Appendix C). All analyses were run in SPSS separately for each measure and testwise Bonferroni confidence interval adjustment was used for comparisons of main effects. Both Games-Howell and Hochberg's GT2 post hoc tests for different sample sizes were run (Field, 2013). Effect sizes (Cohen's d) were also calculated and reported in Ap-

¹ <http://www.millisecond.com>

pendix C. A principal axis factor analysis (FA) was conducted on nine variables (IRI-EC, IRI-FS, IRI-PT, IRI-PD; EQ-SS, EQ-CE, EQ-ER; ECS; HAS) which generated three latent variables. Analyses of multivariate (MANOVAs) were used to establish differences between groups on the three latent variables.

4.4 Results

4.4.1 Between Group Differences: One-Way ANOVAs

There were significant group differences on ECS [$F(2, 122) = 5.281, p = 0.006, \eta^2 = 0.08$], both sensory-localised and affective-general groups scored higher than controls ($S/L : p = 0.028, A/G : p = 0.034$) but did not differ from each other ($p = 0.915$). There was a significant group difference on the emotional reactivity subscale of the EQ [$F(2, 122) = 5.247, p = 0.007, \eta^2 = 0.08$], with both sensory-localised and affective-general groups scored higher than controls ($S/L : p = 0.02, A/G : p = 0.05$) but not different from each other ($p = 0.99$). None of the other subscales of the EQ showed differences between groups: Cognitive Empathy [$F(2, 122) = 2.297, p = 0.105, \eta^2 = 0.031$] and SSs [$F(2, 122) = 0.370, p = 0.695, \eta^2 = 0.006$]. The results of the questionnaire measures are summarized in Figure 4.1. IRI scores did not show any significant differences on Personal Distress [$F(2, 122) = 0.296, p = 0.744, \eta^2 = 0.005$] or in empathic concern [$F(2, 122) = 0.296, p = 0.141, \eta^2 = 0.032$] but there was a trend toward increased scores in vicarious perceivers for perspective taking [$F(2, 122) = 2.930, p = 0.057, \eta^2 = 0.046$] and fantasy [$F(2, 122) = 2.981, p = 0.054, \eta^2 = 0.047$] subscales.

The HAS revealed no significant differences between groups [$F(2, 122) = 2.576, p = 0.08, \eta^2 = 0.041$].

4.4.2 Between Group Differences: Factor Analysis and MANOVAs

A principal axis factor analysis (FA) was conducted on nine variables with oblique rotation (direct oblimin). The Kaiser–Meyer–Olkin measure verified the sampling adequacy for the analysis, KMO = 0.741 and all KMO values for individual variables were greater

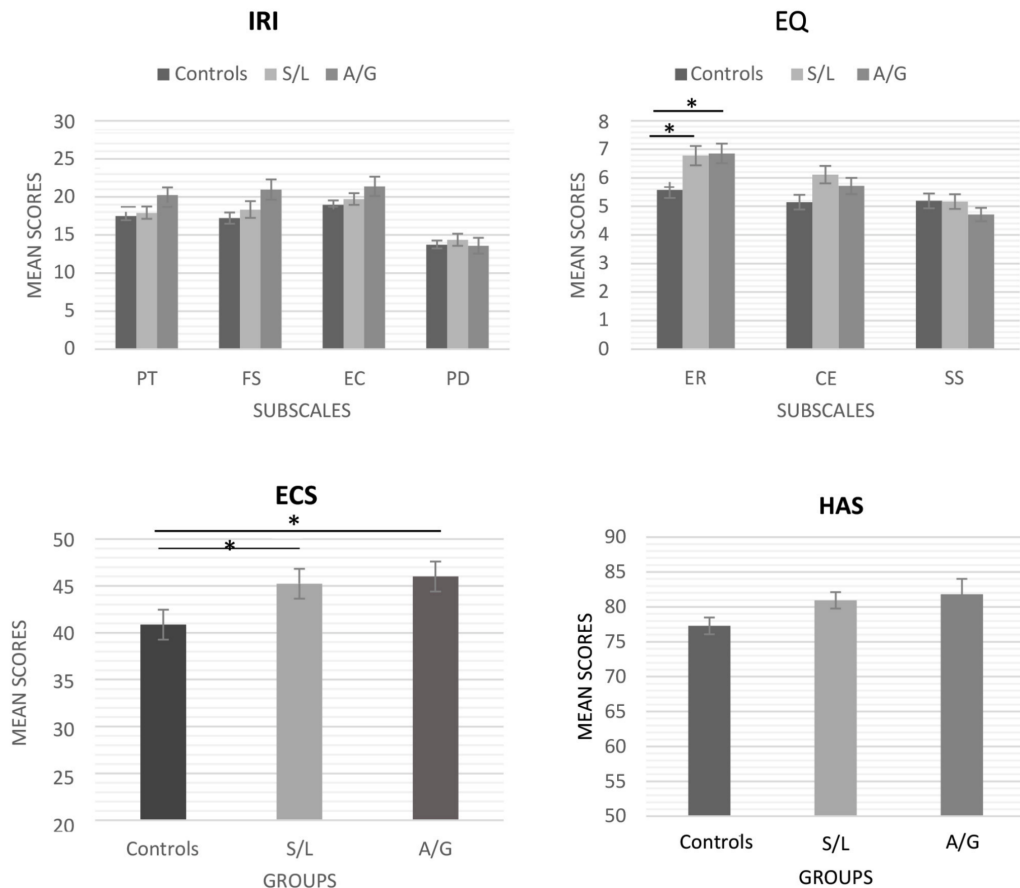


Figure 4.1: IRI, EQ, ECS, and HAS scores. S/L, sensory-localised; A/G, affective-general. Both S/L and A/G scored higher on emotional contagion (ECS) and emotional reactivity (EQ-ER) than controls but not on cognitive empathy (EQ-CE) or social skills (EQ-SS) subscales. No significant differences were found on IRI and HAS. Error bars indicate ± 1 SE. ($p < 0.05$)

than the acceptable limit of 0.5 (Kaiser, 1974). An initial analysis was run to obtain eigenvalues for each factor in the data. Three factors had eigenvalues over Kaiser's criterion of 1 and in combination explained 64.8% of the variance. The scree plot was ambiguous and showed inflections that would justify retaining both two or three factors (Field, 2013). We retained three factors because of the convergence of the scree plot and Kaiser's criterion on this value. IRI-EC, IRI-PT, and IRI-FS clustered on factor 1, EQ-SS, EQ-CE, and IRI-PD clustered on factor 2, EQ-ER, ECS, and HAS clustered on factor three. Thus, we distinguished between three underlying latent variables: interpersonal and imaginary abilities (Factor 1), low emotion regulation (Factor 2), and socially elicited emotional states (Factor 3). The results can be seen in Table 4.1.

The three latent variables identified by FA were included in a multivariate analysis of variance (MANOVA). All variables respected the assumption of normality, the only ex-

Table 4.1: Factor analysis results

Rotated factor loadings			
Variable	Interpersonal and imaginary abilities	Low emotion regulation	Socially elicited emotional states
IRI_EC	0.81	0.03	-0.01
IRI_FS	0.79	-0.06	-0.18
IRI_PT	0.75	0.06	0.25
EQ_CE	0.10	-0.77	0.23
EQ_SS	0.05	-0.74	0.13
IRI_PD	0.20	0.64	0.45
ECS	-0.22	0.03	0.88
EQ_ER	0.25	-0.22	0.69
HAS	0.19	-0.23	0.56
Eigenvalues	3.12	1.5	1.20
% of variance	34.67	16.64	13.35

Values in bold indicate the highest loadings on each factor.

ception being the interpersonal and imaginary ability variable in the A/G (Shapiro–Wilk test, $p = 0.04$). Two outliers were excluded from the A/G group and the Box’s test confirmed the assumption of equal covariance ($p = 0.08$). Pillai’s trace multivariate test revealed significant effect $F(3,238) = 3.663$, $p = 0.002$ and separate univariate tests showed that there was a significant differences between groups on interpersonal and imaginary abilities $F(2,129) = 4.781$, $p = 0.01$ and on socially elicited emotional states $F(2,120) = 8.122$, $p < 0.001$ but not on low emotion regulation $F(2,120) = 1.181$, $p = 0.311$. Post hoc tests indicated that the A/G group scored higher than controls on the interpersonal and imaginary ability ($p = 0.007$) but there was no difference between S/L and controls ($p = 0.66$). Both S/L and A/G groups scored higher on socially elicited emotional states ($p = 0.008$, $p = 0.003$ respectively). There were no differences between the two groups or between the two groups and controls in emotion regulation (S/L vs. C, $p = 0.35$; A/G vs. C, $p = 0.99$; S/L vs. A/G, $p = 0.67$).

4.4.3 Self-Other Associations

The Individualism-Collectivism Interpersonal Assessment (ICIAI) was analyzed as a 3*4 mixed ANOVA contrasting group (control, S/L, A/G) and closeness (family, friend, col-

league, stranger). There was a main effect of closeness [$F(3, 122) = 246.405, p < 0.001, \eta^2 = 0.669$] but there was no main effect of group [$F(2, 122) = 0.619, p = 0.941, \eta^2 = 0.001$] or interaction [$F(6, 122) = 0.536, p = 0.949, \eta^2 = 0.003$]. At a behavioral level, the self-other association task was analysed as a 3*3 mixed ANOVA contrasting group (control, S/L, A/G) and closeness (self, friend, stranger) on response times to correctly endorse matching pairs (see (Sui et al., 2012)). There was a significant effect of closeness [$F(2, 94) = 29.818, p < 0.001, \eta^2 = 0.241$] but no main effect of group [$F(2, 94) = 0.600, p = 0.551, \eta^2 = 0.013$] and no interaction [$F(4, 1.940) = 0.134, p = 0.781, \eta^2 = 0.009$] (see Figure 4.2).

All together, these results indicate that vicarious pain responders have heightened socially elicited emotional states but none of the groups differ from controls on emotion regulation and neither on subjective (as measured by ICIAI) or objective (as measured by the task) self-other associations. Overall, vicarious pain responders seem to have higher emotional responsiveness than non- responders but no differences in emotion regulation or their reports with others.

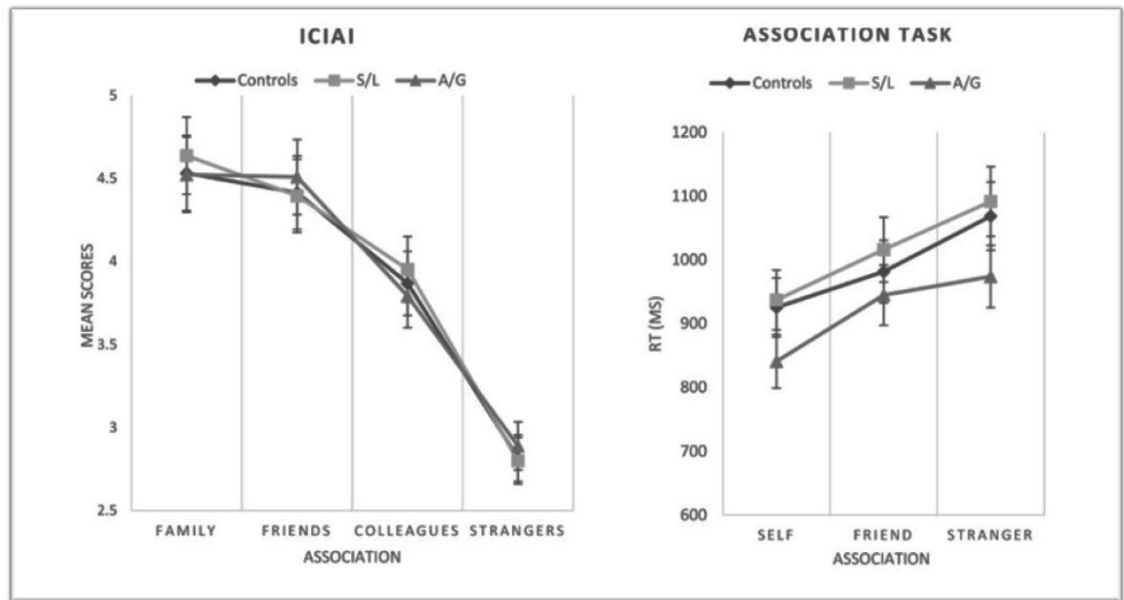


Figure 4.2: ICIAI and self-other association task results. S/L, sensory-localised; A/G, general affective. The effects of closeness appear both in subjective scores and in task reaction times but not as an effect of group. All groups show a similar trend in RTs to the self-other association. Error bars indicate ± 1 SE.

4.5 Discussion

The capacity to co-represent the feelings of other people has a central role in most theoretical accounts of empathy (De Vignemont and Singer, 2006; Lockwood, 2016). However, the mechanism by which this occurs remains under debate as does its relationship to social behaviour. For instance, whilst empathy may underpin acts of compassion (Singer and Klimecki, 2014) it has also been claimed that too much empathy can be detrimental (Bloom, 2017). In the present study, we took advantage of a recently reported individual difference in the neurotypical population; namely, the extent to which people report consciously feeling pain when observing other people in pain. Some people report feeling the pain of others either localised on the corresponding part of their own body (Sensory-Localised responders, S/L) or a non-localised, more general body feeling (Affective-General responders, A/G). However, the majority of people report no conscious feelings of pain: they either have an implicit simulation or possibly do not simulate the pain of others. In this study, we assessed for the first time how these individual differences in vicarious pain are linked to differences in various dimensions of empathy and relationships with others. We employed a series of questionnaires to test between groups differences and, given the multitude of variables used, we also ran a factor analysis which showed that there were three underlying latent variables: socially elicited emotional states (ECS, EQ-ER, and HAS), interpersonal and imaginary abilities (IRI: PT, EC and FT), and low emotion regulation (EQ-SS, EQ-CE, IRI-PD).

4.5.1 Socially Elicited Emotional States

Both S/L and A/G vicarious pain responders report a greater perception of socially elicited emotional states. This suggests that vicarious pain perception is probably just one trait of a much broader phenotype in conscious vicarious pain responders (including emotion contagion as well as the defining symptom of ‘pain contagion’). Moreover, the socially elicited emotional states variable includes both measures of emotional responsiveness and helping behaviours. HAS loaded on the same latent variable as emotional reactivity/contagion indicating that higher responsiveness to others’ emotions is linked to a helpful behaviour rather than an avoidant one. This may be explained by the fact that

that helping someone leads to a change in the emotional state of the helper, as some of the HAS items point out (e.g. 'It feels wonderful to assist others in need') which would be more noticeable in people with elevated emotional contagion. Since there were no differences recorded in the other variables, this behaviour may also be mediated by their intact social-cognitive skills and their ability to distinguish between self and other (Bird and Viding, 2014).

4.5.2 Low Emotion Regulation

Despite having shared representations of pain and enhanced affective empathy, vicarious pain responders did not report enhanced social skills and neither personal distress. It seems like these behaviours are neither impaired nor stimulated by strong emotional responses as previously stated by Bloom (2017) (N.B. we only recorded general, trait attitudes in this study and not immediate responses to painful stimulation). Interestingly, social and cognitive skills (the two EQ subscales) and personal distress (the IRI subscale) loaded on the same factor showing that the more personal distress someone reports, the lower his/her social – cognitive skills are. Thus, impaired social- cognitive skills lead to higher levels of personal distress and the capacity to regulate emotions seems to be mainly linked to poor social-cognitive skills rather than high emotional responsiveness. Vicarious pain responders are characterised by higher socially elicited emotional states, but they have typical social-cognitive skills and emotion regulation suggesting that the mechanisms for these different empathic qualities could be segregated and function independently, but they are not fully understood yet.

Reporting feeling the pain of others does not seem to impact in any way their ability to relate to the other or their levels of personal distress. In the wider literature, symptoms such as emotional contagion are regarded as developmental precursors of empathy, which are diminished as emotional regulation mechanisms mature (Thompson, 1991; Eisenberg, 2000). People with vicarious pain appear to have retained a high capacity for emotional contagion but without reporting a concomitant problem in regulating or coping with these symptoms. Osborn and Derbyshire (2010) also reported that, in vicarious pain responders, there was no correlation between vicarious pain intensity and personal distress. The fact that vicarious pain perceivers do not have higher levels of

personal distress may be due to habituation to pain which sometimes is noticed in response to frequent exposure to pain (Bingel et al., 2007) or to the fact that they developed a response mechanism towards occurrence of pain. Thus, a testable prediction is that these populations would have better emotional regulation which would be recorded in both questionnaires and physiological measures such as heart-rate variability (Appelhans and Luecken, 2006) and would shed more light on bodily and emotional processing in vicarious pain responders.

4.5.3 Interpersonal and Imaginary Abilities

Three of the scales of the IRI (empathic concern, perspective taking, and fantasy) were found to be associated together, and the A/G group scored significantly higher on this factor. These measures tend to reflect a more deliberate empathic style (e.g., choosing to take another person's perspective) than the emotional contagion/reactivity measures already discussed (which were elevated in both responder groups and with larger effect sizes). Further studies combining behavioral and neuroscientific measures in these groups are needed to establish what underpins this. Previous research indicated that individual differences in perspective taking (PT subscale of IRI) and empathic concern (EC subscale of IRI) influence the feeling of being touched (Bolognini et al., 2013b). Experimentally induced excitability over somatosensory cortex can elicit synaesthetic mirror-touch ((Bolognini et al., 2013b,a), but also see Bowling and Banissy (2017)), a phenomenon similar to mirror-pain responses of the S/L group (see Ward et al. (2018)). However, whilst these studies found that the IRI predicted tactile sensations in their sample (likely comprising non-responders), the IRI was not elevated in the S/L group, but in the A/G group.

With regards to perspective taking, Derbyshire et al. (2013) found that vicarious pain responders were more influenced by the visual perspective of an avatar when judging from their own viewpoint (but they did not distinguish between different kinds of responders). Bucchioni et al. (2016) showed that motor-evoked responses are inhibited more when participants observe the pain from a first - person perspective than from a third-person perspective (hand that receives the pain is rotated at 180°). If vicarious pain responders are more influenced by a third perspective, then we would expect them to

show greater inhibition of motor evoked responses in this condition too.

4.5.4 Self-Other Associations

There were no differences in self-other associations between vicarious pain responders and controls. In both the subjective (ICIAI questionnaire) and objective (self-other association task) measures, we would have expected a linear trend showing that vicarious pain responders treated unknown others as close ones or as self. The results did not confirm this hypothesis. The ICIAI has a strong cultural component (Matsumoto et al., 1997) whilst the self-other association task requires an abstract association and records reaction times to congruent or incongruent association between a geometrical shape and a label. The task mainly determines changes in perceptual saliency by employing various self- other associations and the use of self-associated labels. Importantly this type of task does not require participants to engage in online control of self-other representations. That is to say that participants do not have to co-represent themselves and others in the same trial because they are cued toward self or other, and thus it is unlikely that self or other are represented at the same time (i.e., only the self or other is represented, but not both). Prior work suggests that the online control of co- activated self-other representations is linked to empathy and associated brain networks including the rTPJ (e.g., Santiesteban et al. (2012, 2015); Sowden et al. (2015); Nobusako et al. (2017)), but the ability to attribute mental states to the self or others does not tend to recruit this same brain network (e.g., Lombardo et al. (2010); Sui et al. (2013a,b)). Given that individuals with conscious vicarious pain perception have been shown to differ in their neural profile within the rTPJ (Grice-Jackson et al. (2017a)), it is perhaps more likely that they will differ on tasks that involve the online control of co-activated self-other representations than tasks that tap into the ability to attribute states to the self or others via cues like the one used in the current investigation.

4.5.5 Summary

Overall, our results indicate that vicarious pain responses are mainly linked to heightened socially elicited emotional states and we obtained no evidence for significant differences in emotion regulation or self-other associations. Moreover, differences in perspective

taking and imaginative abilities were only recorded in the A/G group. These results further characterise vicarious pain responders and indicate that consciously feeling the physical pain of another is associated with heightened socially elicited emotional states, but not with low emotion regulation. Thus, the heightened emotional responsiveness observed in vicarious pain responders is mainly associated with a helping rather than avoidant behaviour and good emotion regulation could mediate this mechanism.

Article IV: Differences in Interoceptive Accuracy and Emotion Regulation Distinguish between Affective and Sensory aspects of Feeling the Pain of Others

5.1 Abstract

Vicarious pain responses refer to the ability to physically re-experience someone else's pain, but there is considerable inter-individual variability expressed in the quality of the pain felt. In the present study, we investigated interoceptive and autonomic processes in three distinct groups of vicarious pain responders: controls (people who report no pain when seeing someone else experiencing physical pain), (2) sensory-localized (S/L) responders (report sensory qualities and a localized feeling of pain) and (3) affective-general (A/G) responders (report a generalized and emotional feeling of pain). The aim of the study was to establish if there were any differences between vicarious pain responders and controls in the accuracy of perceiving their cardiac interoceptive signals and in physiological arousal and/or regulation.

Participants completed the State-Trait Anxiety Index (STAI), a cardiac interoceptive accuracy and awareness task and a video-presentation task depicting people suffering intense or mild physical pain and no-pain. Recordings of heart rate, systolic blood pressure (SBP),

and skin conductance response (SCR) were taken during the video-presentation task and at baseline. Results indicated that the A/G group had lower interoceptive accuracy but not awareness whilst the S/L group had higher heart rate variability (HRV), an index of good autonomic emotion regulation. There were no differences between groups in anxiety levels or in the amplitude of SBP and SCR; there was only an effect of condition with observing injections eliciting a higher physiological response than accidents and no-pain. These results are framed within theories linking bodily self-awareness to interoceptive processes and increased HRV to better autonomic regulation. Altogether, these findings indicate that vicarious pain responders have adaptive coping strategies and a salutogenic approach to their bodily feelings.

5.2 Introduction

5.2.1 Vicarious Pain Responders: General Introduction

Seeing someone else in pain may elicit a similar sensation in the observer which is known as vicarious pain perception (Fitzgibbon et al., 2010b, 2012). Vicarious pain experiences have been reported in clinical populations such as patients with a history of traumatic pain or in phantom limb patients (Giummarra and Bradshaw, 2008; Fitzgibbon et al., 2010b), but also in typical populations. Individuals may report feeling pain on their own body when observing others in pain in experimental settings, usually as a response to the presentation of images or videos depicting painful events (Osborn and Derbyshire, 2010; Grice-Jackson et al., 2017a). These conscious pain experiences have been identified in about 30% of the population but there is considerable inter-individual variability expressed in the quality of the pain felt. Grice-Jackson et al. (2017a) identified two subgroups of vicarious pain responders who report different qualities of their vicarious experience. Using a cluster analysis method, they identified a group of sensory-localised vicarious pain responders (S/L) who report feeling a localised pain sensation on their own body when seeing someone else in pain and represent about 17% of the population, and a group of affective-general responders (A/G) who report a generalised pain sensation in their entire body and represent about 10% of the population. Seeing someone else in pain in an fMRI-based paradigm, generates neuronal responses in specific brain regions, most notably the somatosensory cortices, activating sensory-motor processes through mimicry mechanisms which occur even in the absence of conscious pain report (see Lamm et al. (2011) for a metaanalysis). These mechanisms are thought to be more pronounced in vicarious pain/touch responders and, according to the threshold theory (Blakemore et al., 2005; Ward and Banissy, 2015), the overactivity in brain regions involved in mirroring the states of others leads to vicarious brain activation above a threshold for conscious perception. There is a fair amount of evidence supporting this theory with various studies finding increased grey matter density and cortical activity in regions such as the somatosensory cortex (Grice-Jackson et al., 2017a; Holle et al., 2013; Blakemore et al., 2005).

However, other neuronal particularities have been identified in these populations

(e.g. lower density in the rTPJ ([Grice-Jackson et al., 2017a](#); [Holle et al., 2013](#))) supporting a complementary theory: the self-other theory. This theory refers to impairments in the ability to distinguish between self and other which can be manifested in the socio-cognitive domain, in the control of self and other actions or experiences, and in bodily self-other representations.

5.2.2 Bodily self and interoceptive awareness in vicarious pain responders

The ability to distinguish between self and other has been of great interest in studies investigating vicarious perception and there is a fair amount of evidence supporting the idea that vicarious perception is related to differences in bodily self. More precisely, the capacity to mirror the sensory experience (pain or touch) of another person on one's own body may reflect a tendency to treat all observed bodies as self-related and to identify more with the other. [Derbyshire et al. \(2013\)](#) used the RHI paradigm and showed a greater tendency to incorporate the rubber hand in the pain-responders group when compared to controls as recorded by subjective reports (N.B. they did not characterise the pain responders nor divided them into two groups). In a more recent study, [Botan et al. \(2018b\)](#) showed that only the sensory-localised group of vicarious pain responders had a greater tendency to incorporate the rubber hand in both synchronous and asynchronous conditions as recorded by subjective ratings and proprioceptive drifts.

Differences in bodily self-awareness have also been recorded in both groups of vicarious pain responders which reported more depersonalisation-like experiences (i.e. detachment from themselves and their environment) ([Bowling et al., 2019](#)). Interestingly, individuals with more pronounced depersonalisation traits are also more susceptible to body ownership illusions ([Kanayama et al., 2009](#); [Sierra et al., 2002](#)), apparently linked to differences in the primary somatosensory cortex (e.g., [Aspell et al. \(2012\)](#); [Otsuru et al. \(2014\)](#)). This evidence further suggests that the altered sense of bodily self may be associated with atypical somatosensory activity.

Notably, vicarious pain responders score higher on the Multidimensional Assessment of Interoceptive Awareness (MAIA) indicating that they have higher interoceptive sensibility, or awareness of their body ([Bowling et al., 2019](#)). [Mehling et al. \(2012\)](#) defined

interoceptive awareness as the ability to be sensitive and to notice subtle bodily changes and developed MAIA as a measure of it. However, [Garfinkel et al. \(2015a\)](#) proposed three independent dimensions of interoception: sensibility (noticing subtle changes in the body recorded with subjective reports), interoceptive accuracy (performance on heart beating and counting tasks) and awareness (metacognition reported as confidence in the performance on interoceptive tasks). To avoid confusion, we will use the terms and definitions given by [Garfinkel et al. \(2015a\)](#). These three dimensions of interoception are dissociable, they do not correlate with each other and have been differently associated with bodily self-processing ([Garfinkel et al., 2015a](#)).

Vicarious pain responders have higher interoceptive sensibility as measured with subjective reports, however, it is unclear if this also corresponds to higher interoceptive accuracy and/or awareness. Previous studies using MAIA have shown that differences in interoceptive processing seem to be related to emotional susceptibility but completely independent from interoceptive accuracy ([Calì et al., 2015](#)) and, in relation to pain, fibromyalgia patients suffering from chronic pain exhibit a higher tendency to note bodily sensations as suggested by the noticing and non-distracting subscales ([Valenzuela-Moguillansky et al., 2017](#)). These results are in line with [Bowling et al. \(2019\)](#) findings of higher scores in vicarious pain responders on MAIA noticing and non-distracting subscales.

Regarding interoceptive accuracy, previous research has indicated that high interoceptive accuracy is associated with decreased tolerance to pain manifested in lower pain thresholds ([Pollatos et al., 2012](#)) and that it enhances the estimated degree of pain (cognitive empathy), as well as arousal and feelings of compassion (affective empathy), in response to painful pictures ([Grynberg and Pollatos, 2015](#)). Moreover, interoceptive processes have been linked to the bodily-self which arises from the integration of multisensory experiences manifested within the exteroceptive, interoceptive and proprioceptive domains ([Tsakiris, 2017](#)). The focus of this research has been on explaining and further characterising bodily-self processes in vicarious pain responders. To this end, it has investigated the somatosensory (tactile) and proprioceptive particularities in vicarious pain responders through bodily ownership paradigms, but it has not yet considered the interoceptive domain. Importantly, interception has been considered to play a major role in the malleability of the bodily self ([Seth, 2013](#)) and empirical evidence has linked the

suggestibility to bodily ownership paradigms to interoceptive accuracy. Tsakiris et al. (2011) showed that lower interoceptive accuracy is associated with higher susceptibility to the RHI. However, these results have not been fully replicated. Crucianelli et al. (2018) did not find any evidence indicating that the performance on the heartbeat counting task influenced the suggestibility to the RHI paradigm in a sample considerably larger than the one used by Tsakiris et al. (2011) (i.e. 63 versus 46 participants).

Neuroanatomical evidence also points out to a relation between vicarious pain and interoceptive processing. The anterior insular cortex is implicated in mapping internal bodily states and self-related bodily experiences (including pain and touch) (Craig and Craig, 2009; Critchley et al., 2004), in representing emotional arousal (Singer et al., 2009), in processing and expecting noxious stimuli (Coghill et al., 1999; Bornhövd et al., 2002; Sawamoto et al., 2000), and providing the neural basis of interoceptive processing (Critchley et al., 2004; Pollatos et al., 2007). Most importantly, the bilateral anterior insula is activated both when someone experiences pain and when someone observes other's pain (Singer et al., 2004). It mediates the empathic engagement according to individual traits (Singer et al., 2006) and has greater density in vicarious pain responders (Grice-Jackson et al., 2017a). Thus, interoceptive processing, vicarious pain perception, and bodily self-awareness seem to be interconnected processes and may be of particular interest in the study of bodily-self.

Altogether, the evidence connecting vicarious pain responses and interoception is conflicting and we tried to address this gap by measuring both interoceptive accuracy (Schandry, 1981) and awareness (confidence ratings) in the two groups of vicarious responders.

5.2.3 Bodily and emotional processing in vicarious pain responders

Pain sensitivity has been associated with pain anxiety and anxious traits (Palit et al., 2015) and evidence coming from physiological studies shows that anxiety is an important co-variate in the regulation and response of the sympathetic nervous system in vicarious pain responders (Nazarewicz et al., 2015). Moreover, empathic vicarious pain seems to be related to acute distress (Young et al., 2017) and personal distress has been identified

as a good predictor of arousal symptoms as well as a promoter of adaptive empathic skills (Tone and Tully, 2014).

Anxiety has been considered a predictor of pain perception as well as physiological responses to pain in vicarious pain populations (Nazarewicz et al., 2015; Young et al., 2017). In these studies, the authors used anxiety itself as a variable in their analysis to establish the vicarious pain groups which mainly represented two categories: anxious vicarious pain responders and non-anxious vicarious pain responders. Physiological differences (e.g. slower respiration rate, increased heart rate and decreased heart rate variability) were found for the anxious vicarious pain responders. In our research, we take a somewhat different approach of defining the groups of vicarious pain responders based on the phenomenological characteristics of pain (using our previously developed measure), and consider anxiety as a separate individual difference which may, or may not, be a characteristic of one or more of these groups (for previous evidence see Bowling et al. (2019) and Botan et al. (2018a)). In the present study, we took measures of both anxiety state and trait as well as heart rate in order to re-test the predictions that there are no differences in anxious states in vicarious pain responders and that this may be related to better emotion regulation, expressed as an increase in heart rate variability (HRV).

Heart rate variability represents the variability in the interval between successive heartbeats and it is an indicator of cardiac autonomic regulation in responses to stressors (Appelhans and Luecken, 2006; Thayer et al., 2012). Decreased heart rate variability has been associated to a poorer adaptability of the autonomic nervous system, cardiac functioning and health outcomes (Koenig et al., 2016; Tracy et al., 2016) and negatively correlated with increased heart rate (Sacha and Pluta, 2005). Cardiac functioning has been linked to responses to emotional stimuli (including pain) and an increase in heart rate has been often recorded in response to negative emotions including sadness and pain (Miu and Balteş, 2012; Loggia et al., 2011) whilst HRV has also been found to vary according to pain exposure and individual pain thresholds (Appelhans and Luecken, 2008; Meeus et al., 2013; Riganello et al., 2019; Tracy et al., 2018). In our current study design, we recorded HR and HRV at resting state but also during presentations of videos evoking pain and eliciting vicarious responses in the viewers, our prediction being that vicarious pain responders would have higher HRV.

Alongside heart rate measurements, systolic blood pressure (SBP) and skin conductance response (SCR) were recorded as event-related activations during the experiment in order to obtain an indicator of the level of physiological arousal. SBP was recorded as a measure of hyperarousal following a stressful situation (Davydov et al., 2007, 2010; Gasperin et al., 2009) which increases during perception of negative states such as anger or fear (of pain) (Garfinkel et al., 2015b; George et al., 2006; Roberts and Weerts, 1982), or imagery of these negative states (Schwartz et al., 1981). SCR was recorded alongside SBP, as a measure of (vicarious) arousal (Vaughan and Lanzetta, 1980, 1981) which increases in response to both self and vicarious pain and its intensity can predict pro-social behaviour (Hein et al., 2011). Interestingly, SCR responses to arousing stimuli are suppressed in dissociative-experiences conditions such as depersonalisation/derealisation (Dewe et al., 2016; Sierra et al., 2002) which are linked to vicarious pain responses and also in anxiety (Naveteur et al., 2005), a trait that has been previously associated with vicarious pain.

We were mainly interested in the physiological processes associated with vicarious pain responses starting from the assumption that pain elicits an arousal response controlled by the autonomic nervous system and manifested in the sympatho-vagal balance (Koenig et al., 2016). As previously stated, vicarious pain responses are based on mirroring mechanisms which occur at a neuronal and physiological level and are also manifested in mirroring-physiological changes. Thus, they have been linked to autonomic physiological changes similar to autonomic responses experienced in oneself (Levenson and Ruef, 1992). Knowing that vicarious responders experience an intense bodily pain, we would expect a higher increase in their SCR and SBP when compared to controls, but it becomes difficult to predict their response if taking into account possible confounds such as depersonalisation and anxious traits.

Altogether, interoceptive accuracy together with reported levels of anxiety and physiological parameters of arousal (i.e. SPB and SCR) were measured during this experiment in controls and vicarious pain responders. The aim was to record physiological changes in these populations in response to pain presentation and to establish their level of arousal and/or distress as well as their objective sensitivity towards their body. Based on previous research in these sub-groups, our main research questions were: 1) does the higher interoceptive sensibility observed in vicarious pain responders correspond to a higher

interoceptive accuracy and/or awareness?; 2) do vicarious pain responders have better emotion regulation considering the fact that they do not show higher levels of anxiety or personal distress despite having heightened emotional contagion?; and 3) is their intense bodily response to pain caused, at least partly, by an enhanced physiological reactivity to pain?.

5.3 Materials and Methods

5.3.1 Participants

A total of 72 participants (mean age = 21.57, SD = 4.30; 56 females) completed the study. Each participant had previously completed the VPQ online via Qualtrics Online Survey and were divided into three groups following a cluster analysis conducted on a larger dataset of participants (Aged 18–60 years, mean age = 20.11, SD = 6.94; 290 Males, 1004 Females). This was based on the dimensions of mean pain intensity, number of sensory minus affective descriptors, and number of localised minus general responses (following [Botan et al. \(2018b\)](#)). There were 30 participants classed as non-responders (i.e. controls) (mean age = 22.40, SD = 5.47, 22 females), 20 participants classed as sensory-localised (S/L) responders (mean age = 21.45, SD = 3.89, 14 females) and 22 participants classed as affective-general (A/G) responders (mean age = 20.55, SD = 2.32, 20 females). The groups did not differ by age [$F(2, 71) = 1.199, p = 0.308, \eta^2 = 0.034$] or gender ($\chi^2 = 3.238, p = 0.198$).

Due to technical issues, not all data was recorded from all participants: two non-responders did not complete the interoceptive tracking task, one A/G lacked heart rate variability data (HRV), one S/L and two A/G lacked blood pressure data, and one A/G lacked skin conductance data. Additional interoception data was recorded in a previous unpublished experiment using the same methodology from 69 participants (mean age = 22.75, SD = 4.09; 60 females) which included 56 non-responders (controls), 11 S/L responders and two A/G responders ([Grice-Jackson et al., 2017a](#)), classified according to the same cluster analysis as the new participants. Participants were recruited via email invitation or via SONA from Sussex University. Ethical approval was obtained from the Science and Technology Research Ethics Committee of the University of Sussex and all

participants offered their written informed consent at the beginning of the study.

5.3.2 Vicarious Pain Questionnaire

The VPQ is comprised of 16 videos (no audio) of people experiencing physical pain (e.g., falls, sports injuries, injections), each video lasting for 10s (Grice-Jackson et al., 2017a). After each video, participants were questioned if 1) they experienced a bodily sensation of pain; 2) how intense was that pain (1-10 Likert scale); 3) if the pain was localised to the same place, to a different place or generalised to the entire body; and 4) asked to describe the pain selecting various pain adjectives (10 sensory such as ‘tingling,’ ‘burning,’ ‘stinging,’ and 10 affective descriptors such as ‘nauseating,’ ‘gruelling,’ ‘aversive’). These answers were used to generate the three variables (i.e., pain intensity, localized-generalized responses, and sensory – affective responses) entered the two-step cluster analysis. The three groups of vicarious pain responders were generated: controls, sensory-localised (S/L) and affective general (A/G) (for further details see Botan et al. (2018b)).

5.3.3 Interoceptive Accuracy and Awareness

Interoceptive accuracy was measured using the heartbeat tracking task (Schandry, 1981) containing six trials with varying interval durations of 25, 30, 35, 40, 45 and 50 seconds played in a randomised order. Participants were instructed to silently count the number of heartbeats perceived in the given interval and to report them at the end of each trial. Their actual heartbeats were measured with a pulse oximeter. For each trial, the accuracy score was derived using the following formula: $1 - (|nbeats_{real} - nbeats_{reported}|) / ((nbeats_{real} + nbeats_{reported}) / 2)$.

The resulting scores of each trial were averaged yielding the overall value for each participant (Garfinkel et al., 2015a). Confidence judgements were taken at the end of each trial, participants being asked to rate the confidence they had in their reported number of heartbeats. Their response was recorded on a 10 points continuous visual analogue scale (VAS) from ‘total guess/no heartbeat awareness’ to ‘complete confidence/full perception of heartbeat’. Interoceptive awareness was then calculated using the Pearson correlation between interoceptive accuracy and confidence rating (Garfinkel et al., 2015a).

5.3.4 Psychophysiological responses to vicarious pain

The task consisted of 32 film clips: 16 videos showed people in physical and 16 control videos showing people performing regular activities (e.g. riding a bicycle, sitting on a sofa, reading the newspaper etc.). The videos depicting the physical pain were the same used in the Vicarious Pain Questionnaire (VPQ). Half of them contained images with injections and the other half accidents. All clips lasted for 10s and their order was randomised. A jittered inter-stimulus interval (ISI) of 5s, 10s or 15s represented by a grey screen with a fixation cross followed each video. The task was presented on a computer screen placed in front of the participants using Cogent2000¹ (version 1.32) in Matlab (R2013a, Mathworks). The design of the task can be seen in Figure 5.1b.

5.3.5 Physiological Measures

All physiological measures were recorded using with Cambridge Electronic Design (CED) hardware and Spike2 physiological recording software (version 7.17) at a sampling rate of 1000Hz, interfacing physiological recording with the task in Matlab. Measurements set-up and recording can be seen in Figure 5.1a.

Heart Rate and Heart Rate Variability

Cardiac cycles were recorded using electroencephalography (ECG, CED1902-11/ECG), with 10Hz high bandpass filter and 100 Hz low bandpass filter applied (Fedotov, 2016), consisting of three electrodes: two placed under the lower clavicle on the right and left side respectively and one (the ground electrode) placed on the back of the participant. For the analysis, a threshold was applied to isolate R-wave peaks and to extract the number of heartbeats in a given time interval. The heartbeats were extracted for pain videos, control videos, and three minutes resting state period taken at the end of the task. This gave measures of heart rate (HR) (beats per time interval) and heart rate variability (HRV) expressed as the root mean square of successive differences (RMSSD) between normal heartbeats, the primary time-domain measure for short-term variation, strongly correlated with high-frequency variations and an indicator of the vagally me-

¹ http://www.vislab.ucl.ac.uk/cogent_2000.php

diated (parasympathetic) changes reflected in HRV (Shaffer and Ginsberg, 2017). Both HR and HRV were calculated for injection videos, accident videos, control videos and resting state.

Blood Pressure

Blood pressure was recorded using photoplethysmographic technology (Finometer PRO; Finapres 2300, Ohmeda, Eaglewood, CO, USA) using an inflatable finger cuff and infrared plethysmograph attached to the index finger of the participant's left hand. Beat-to-beat values of systolic blood-pressure (mmHg) were recorded and smoothed using Spike 2.7.17 channel process function, creating a constant signal of systolic peaks. Mean systolic blood pressure levels were then derived by averaging systolic levels over accident videos, injection videos, control videos and resting state (Garfinkel et al., 2015b).

Skin Conductance Response

Skin conductance was recorded using two finger electrodes (CED2502) placed on the index and middle finger of the participant's right hand. Analysis were performed in Matlab using Ledalab (V3.4.9) software. Adaptive data smoothing was applied, and continuous decomposition analysis was performed with extraction of continuous phasic and tonic activity. Event-related activation was computed for each type of stimulus events: accidents, injections, and control videos as the sum of SCR-amplitudes of SCRs greater than 0.02MuS within a time window of 1-4s of stimulus onset. The data was transformed in order to obtain a more normal distribution using the formula $\log_{10}(\text{SCR}+1)$.

5.3.6 Anxiety Questionnaire. State-Trait Anxiety Inventory (STAI)

The State-Trait Anxiety Inventory (STAI) (Spielberger et al., 1983) is a 40-item self-report scale which assesses both state and trait anxiety. State anxiety items (N=20) assess how participants feel and that precise moment (i.e. '*indicate how you feel right now*') and include statements such as: *I am calm.*, *I feel tense.*, or *I am frightened.* Trait anxiety items (N=20) assess the dispositional, or more stable, trait of anxiety proneness (i.e. '*indicate*

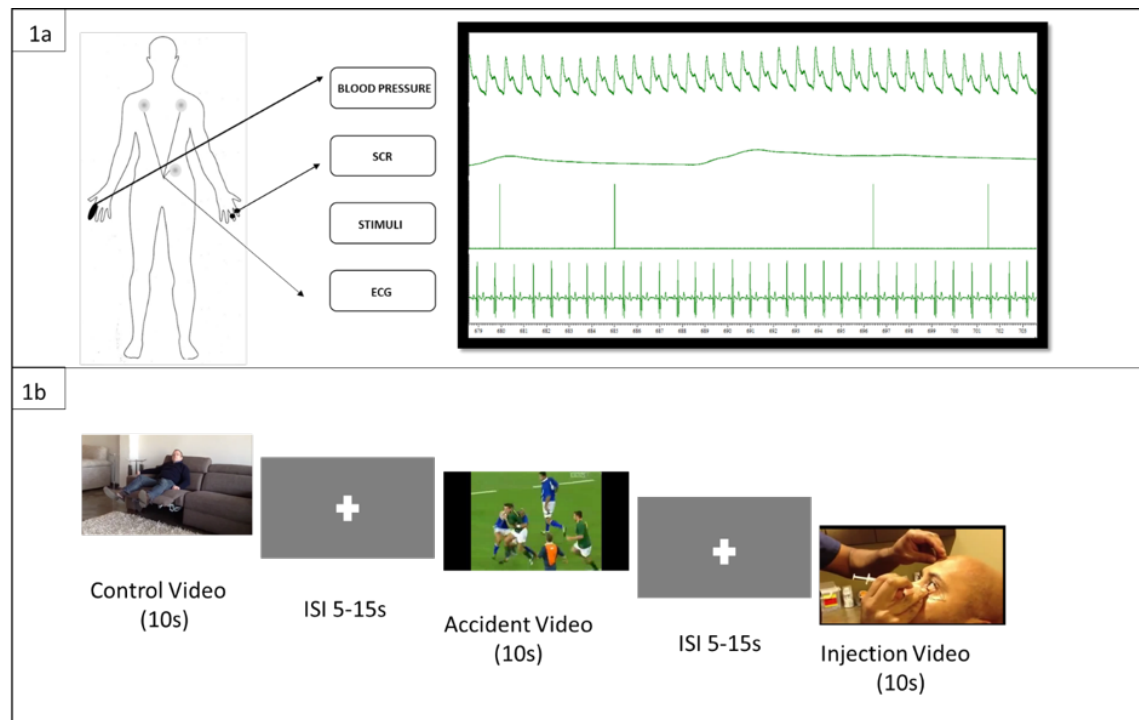


Figure 5.1: a) Recording set-up and interface; b) Task set-up.

how you generally feel’). It contains items such as: *I feel nervous and restless* or *I feel satisfied with myself*. For both state and trait scales, respondents are asked to indicate to what degree the item describes their feelings on a 4-point Likert-type scale ranging from 1 = not at all and 4 = very much so. The questionnaire was administered immediately after participants finished watching the videos.

5.3.7 Statistical Data Analyses

Analyses of variance (one-way ANOVAs) were used to establish differences between groups on unidimensional measures including the interoceptive accuracy and awareness scores, anxiety scores and resting state measures of heart rate and heart rate variability. Mixed models analyses of variance (3×3 mixed ANOVAs) were run for task measures of HR, HRV, blood pressure, and skin conductance. The analyses assessed the interactions between the 3 groups (C, S/L, and A/G) and 3 conditions (control videos, accident videos, and injection videos). When sphericity was not assumed, the most conservative Greenhouse-Geisser correction was reported (Field, 2013).

Variables were treated as continuous and most of them were normally distributed as shown by Shapiro–Wilk tests and Kolmogorov–Smirnov tests. When normality as-

assumptions were violated in more than one group, Kruskal–Wallis H and Mann–Whitney U non-parametric tests were also run, reconfirming the results as shown in Appendix D. These cases included interoceptive accuracy scores and task heart rate data and skin conductance data. All analyses were run in SPSS separately for each measure and test wise Bonferroni confidence interval adjustment was used for comparisons of main effects and Hochberg’s GT2 post hoc tests for different sample sizes were run (Field, 2013). Given the multitude of measures and possible interdependency between them (e.g. possible link between anxiety and physiological responses), supplementary correlation and hierarchical multiple regression analyses were run. In the case of hierarchical multiple analyses, collinearity statistics were all within accepted limits (i.e. Tolerance scores were all > 0.2 whilst VIF scores < 4) (Hair et al., 2013). Durbin Watson test results were all situated between 2 and 2.5 indicating no autocorrelation of residuals. Residual and scatter plots indicated the assumptions of normality, linearity and homoscedasticity were mostly satisfied (Pallant, 2001).

The sample size was based on previous publications investigating differences in physiological processes in vicarious pain responders (Nazarewicz et al., 2015; Young et al., 2017). Based on these findings, effect sizes in physiological reactivity in vicarious pain responders have been relatively large with partial η^2 reaching 0.14². A-priori power analyses conducted with G-power calculator setting the effect size at 0.42, alpha at 0.5, and power at 0.8 indicated a total sample size of 93, approximately 31 participants in each group. This number was reached for the non-responder group, but not for the responder groups due to difficulties in recruiting them. A-posteriori power calculations showed an observed power of 0.9 for interoceptive data (which benefitted from extra participants), 0.5 for HRV data, and 0.3 for BP and SCR data. These two last results were clearly non-significant, however future studies with greater power should try to replicate them.

² <http://imaging.mrc-cbu.cam.ac.uk/statswiki/FAQ/effectSize>

5.4 Results

5.4.1 Interoceptive accuracy and awareness

Interoceptive accuracy and awareness scores can be seen in Figure 5.2. There were significant group differences in interoceptive accuracy ($F(2, 137) = 12.960, p < 0.001, \eta^2 = 0.161$), the A/G group having lower interoceptive accuracy than both controls ($p < 0.001, d = 1.01$) and S/L ($p < 0.001, d = 0.78$). Both results passed the new significance value set at $\alpha = 0.016$ after adjusting for Bonferroni comparisons ($0.05 / 3$ group comparisons). There were no group differences in interoceptive awareness ($F(2, 139) = 1.692, p = 0.188, \eta^2 = 0.024$).

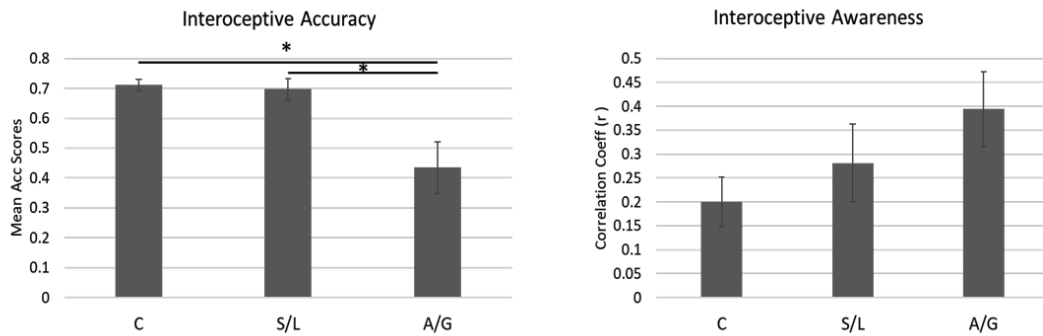


Figure 5.2: Interoceptive accuracy and awareness scores. Error bars indicate $\pm 1SE$. * $p < 0.01$.

5.4.2 Heart Rate (HR) and Heart Rate Variability (HRV)

There were no differences between groups in resting state HR ($F(2, 68) = 1.528, p = 0.224, \eta^2 = 0.044$) nor HRV ($F(2, 70) = 1.314, p = 0.275, \eta^2 = 0.037$). However, the S/L group showed a trend towards lower HR and higher HRV (see figure 3). Regarding task-related HR, mixed model 3×3 ANOVAs showed a significant effect of condition ($F(1.659, 109.491) = 39.859, p < 0.001, \eta^2 = 0.377$) with control videos having lower HR than accident videos ($p < 0.001$) and injection videos ($p < 0.001$) and accident videos having lower HR than injection videos ($p < 0.001$). There was no effect of group ($F(2, 66) = 0.059, p = 0.943, \eta^2 = 0.002$) nor interaction ($F(3.318, 109.491) = 0.634, p = 0.610, \eta^2 = 0.019$). Regarding task-related HRV, mixed model 3×3 ANOVAs showed a significant effect of group ($F(2, 68) = 3.230, p = 0.046, \eta^2 = 0.087$) with

S/L group having higher HRV than the control group ($p=0.045$, $d=0.67$), but this would not survive Bonferroni corrections set at $\alpha=0.005$ (i.e. $0.05/9$ (3conditions \times 3groups)). Importantly, this was still a significant predictor at all stages of the multiple regression analysis presented in section 5.4.6. There was no effect of condition ($F(2, 136) = 0.759$, $p = 0.470$, $\eta^2 = 0.011$) nor interaction ($F(4, 136) = 1.223$, $p = 0.305$, $\eta^2 = 0.035$) (see Figure 5.3).

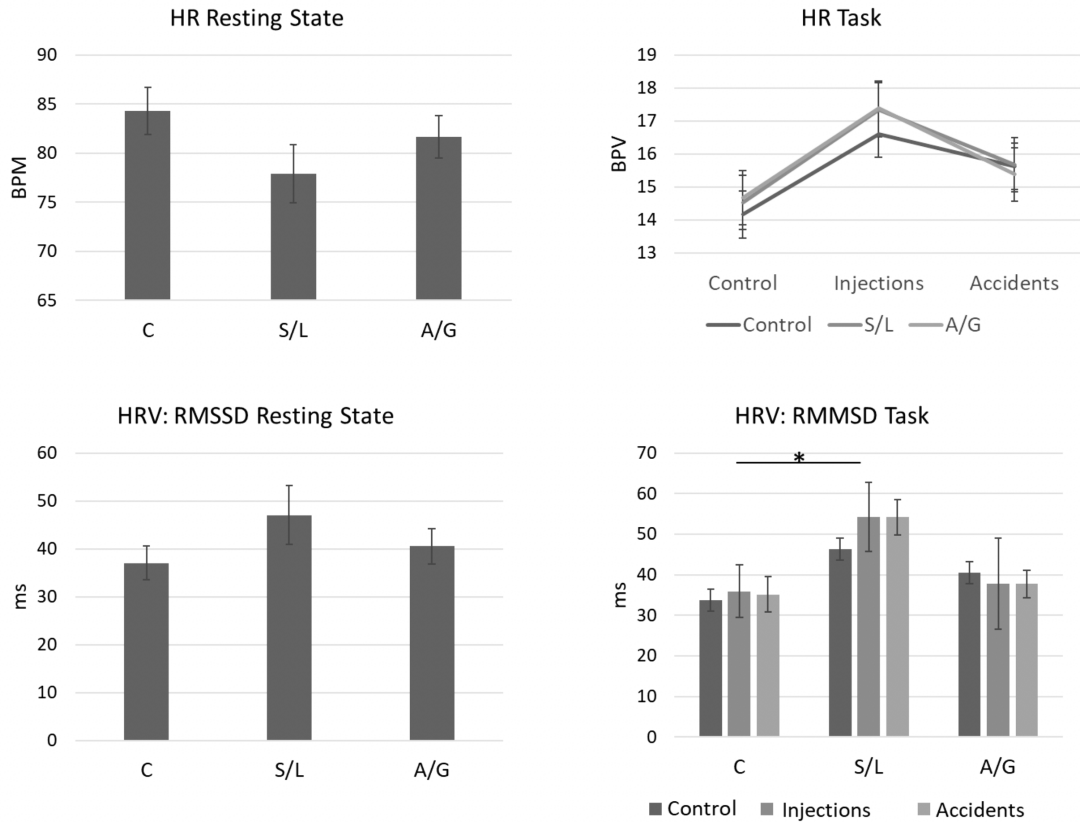


Figure 5.3: Heart Rate (HR) at resting state as beats per minute (BPM) and during the task as beats per 10s video (BPV) for each pain category and control in the upper part of the figure. Heart rate variability (HRV) as RMSSD expressed in milliseconds (ms) at resting state and during the task in the lower part of the figure. Main effect of group for task HRV with S/L group having higher HRV than controls. Error bars indicate $\pm 1SE$. * $p < 0.05$.

5.4.3 Blood Pressure

There was a significant effect of condition in blood pressure ($F(2, 132) = 11.235$, $p < 0.001$, $\eta^2 = 0.145$), the average blood pressure being higher for injection videos when compared to both control videos ($p < 0.001$) and accident videos ($p = 0.002$). There was no effect of group ($F(2, 66) = 1.458$, $p = 0.240$, $\eta^2 = 0.042$) nor interaction ($F(4, 132) =$

1.076, $p = 0.371$, $\eta^2 = 0.032$). A/G group showed a general tendency towards higher blood pressure for all conditions. Results can be seen in Figure 5.4.

5.4.4 Skin Conductance

There was a significant effect of condition in skin conductance ($F(2, 136) = 13.260$, $p < 0.001$, $\eta^2 = 0.163$). The average amplitude in skin conductance response was higher for injection videos than control videos ($p < 0.001$) and accident videos ($p = 0.001$). There was no effect of group ($F(2, 68) = 0.738$, $p = 0.482$, $\eta^2 = 0.021$) nor interaction ($F(4, 136) = 0.419$, $p = 0.795$, $\eta^2 = 0.012$). Results can be seen in Figure 5.4.

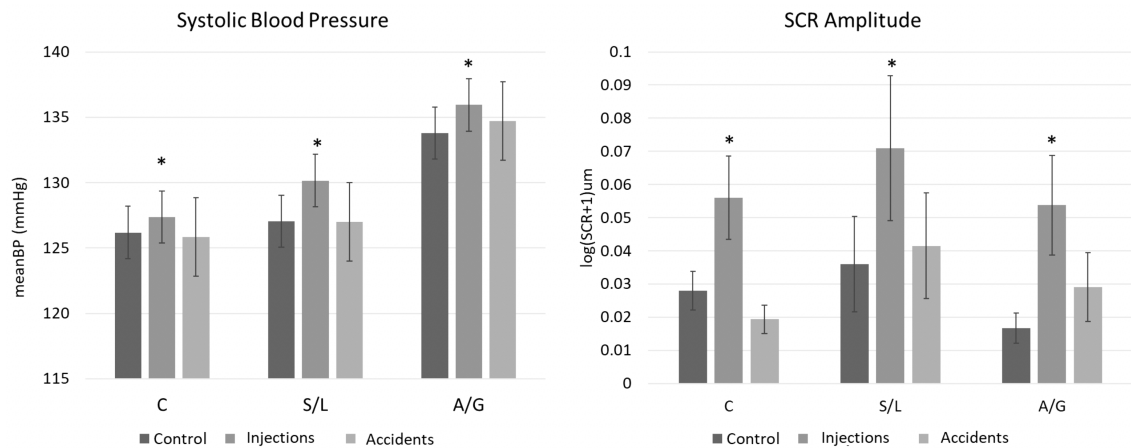


Figure 5.4: Mean systolic blood pressure and skin conductance results. There was a main effect of condition for both measures with injection videos showing increased physiological arousal than both accident videos and control videos. Error bars indicate $\pm 1SE$. * $p < 0.01$

5.4.5 Anxiety Results and Trait measures correlations

There were no differences between groups in neither anxiety state ($F(2, 63) = 0.727$, $p = 0.488$, $\eta^2 = 0.023$) nor trait ($F(2, 63) = 1.494$, $p = 0.232$, $\eta^2 = 0.047$), as previously recorded (Bowling et al., 2019). Anxiety did not correlate with any of the interoceptive or physiological measures. A strong negative correlation was seen between HRV and HR. Correlations can be seen in Table 5.1.

Table 5.1: Correlations between HR, HRV, Anxiety and Interoception

	Interoceptive Accuracy	Interoceptive Awareness	Anxiety State	Anxiety Trait	HR (bmp)	HRV RMSSD
Interoceptive Accuracy						
Interoceptive Awareness	r = 0.046 p = 0.706					
Anxiety State	r = 0.030 p = 0.817	r = - 0.065 p = 0.610				
Anxiety Trait	r = 0.013 p = 0.921	r = - 0.051 p = 0.690	r = 0.599 p <0.001			
HR (bmp)	r = - 0.126 p = 0.311	r = - 0.082 p = 0.510	r = 0.111 p = 0.392	r = 0.244 p = 0.056		
HRV RMSSD	r = 0.189 p = 0.120	r = -0.005 p = 0.969	r = 0.111 p = 0.388	r = - 0.032 p = 0.802	r = - 0.569 p <0.001	

5.4.6 Hierarchical Multiple Regression Models for main outcome variables

Hierarchical multiple regression models were run for the main outcome variables: interoceptive accuracy, HRV, BP, and SCR in pain condition. The group was added at the first step followed by age and gender and anxiety state and trait. For interoceptive accuracy, HR and HRV were also added as a fourth step (Zamariola et al., 2018) and BP as a fifth step (O'Brien et al., 1998). For HRV, HR was added as a predictor in the fourth step of the analysis (Sacha and Pluta, 2005).

As indicated in Table 5.2, the first model of the hierarchical multiple regression including the groups as predictors contributed significantly to the regression model, $F(2,56) = 4.001$, $p = .024$) and accounted for 12.5% of the variation in interoceptive accuracy. Adding the other variables explained an additional 5.3% of the variation and this was not significant.

As indicated in Table 5.3, the first model of the hierarchical multiple regression including the groups as predictors contributed significantly to the regression model, $F(2,59) = 4.117$, $p = .021$) and accounted for 12.2% of the variation in HRV. Adding the other variables explained an additional 31.5% of the variation and this change in R^2 was significant. The S/L group was a significant predictor at all stages of the analysis and HR was a significant predictor when added at stage four.

Table 5.2: Summary of hierarchical regression analysis for variables predicting interoceptive accuracy (* $p < 0.05$; ** $p < 0.01$)

	Model 1			Model 2			Model 3			Model 4			Model 5		
Variables	B	SE B	β	B	SE B	β	B	SE B	β	B	SE B	β	B	SE B	β
S/L Group	-.048	.107	-.063	-.024	.112	-.032	-.026	.119	-.034	-.040	.122	-.052	-.040	.124	-.052
A/G Group	-.277	.103	-.378**	-.248	.106	-.338*	-.253	.110	-.346*	-.248	.115	-.339*	-.249	.119	-.340*
Gender				-.025	.115	-.029	-.011	.122	-.013	-.041	.125	-.048	-.041	.126	-.048
Age				.012	.010	.162	.011	.011	.152	.012	.011	.155	.012	.011	.155
Anxiety State							.003	.008	.060	.000	.008	.009	.000	.008	.008
Anxiety Trait							.0004	.006	.001	.001	.006	.032	.001	.006	.034
HRV										.003	.003	.207	.003	.003	.206
HR										.000	.005	.016	.000	.005	.014
BP													.000	.003	.006
R2		.125			0.149			.152			.188			.188	
F for change in R2		4.001*			2.355			1.551			1.447			1.261	

Table 5.3: Summary of hierarchical regression analysis for variables predicting heart rate variability (HRV) in the pain condition (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$)

	Model 1			Model 2			Model 3			Model 4		
Variables	B	SE B	β	B	SE B	β	B	SE B	β	B	SE B	β
S/L Group	20.840	7.594	.376**	19.814	7.283	.358*	20.934	7.863	.378**	13.709	6.819	.284*
A/G Group	3.720	7.283	.070	6.475	7.351	.122	6.352	7.489	.120	-.620	6.499	-.012
Gender				14.218	7.737	.230	15.235	8.023	.247	6.894	7.005	.112
Age				.427	.695	.077	.436	.717	.078	-.427	.633	-.077
Anxiety State							.058	.499	.018	.020	.422	.006
Anxiety Trait							.280	.408	.107	.546	.350	.209
HR										-1.118	.234	-.563***
R^2		.122			0.185			.198			.437	
F for change in R^2		4.117*			3.231*			2.264			5.984***	

Table 5.4: Summary of hierarchical regression analysis for variables predicting blood pressure in the pain condition

	Model 1			Model 2			Model 3		
Variables	B	SE B	β	B	SE B	β	B	SE B	β
S/L Group	2.088	5.748	.052	2.702	5.922	.067	1.001	6.101	.025
A/G Group	9.475	5.584	.243	8.940	5.804	.230	8.170	5.873	.210
Gender				-5.019	6.039	-.112	-4.524	6.193	-.101
Age				.023	.542	.006	-.093	.555	-.023
Anxiety State							.346	.384	.150
Anxiety Trait							-.399	.318	-.209
R^2		.050			0.062			.089	
F for change in R^2		1.542			.930			.883	

Table 5.5: Summary of hierarchical regression analysis for variables predicting blood pressure in the pain condition

	Model 1			Model 2			Model 3		
Variables	B	SE B	β	B	SE B	β	B	SE B	β
S/L Group	0.17	0.20	.125	.009	.020	.069	.008	.020	.055
A/G Group	.007	.019	.053	.000	.020	-.029	-.004	.020	-.029
Gender				.028	.021	.179	.028	.021	.179
Age				-.004	.002	-.282*	-.004	.002	-.316*
Anxiety State							.002	.001	.222
Anxiety Trait							-.001	.001	-.079
R^2		.012			.029			.030	
F for change in R^2		.375			1.469			1.230	

In the case of SBP, none of the models accounted for a significant variation, not even anxiety (see Table 5.4). None of the models accounted for significant variation in pain SCR. However, age was a significant predictor when added at stages two and three indicating a decrease in SCR responsiveness with age (see Table 5.5), this being in line with some of the previous findings (e.g. (Barontini et al., 1997; Gavazzeni et al., 2008)). The influence of age on SCR is beyond the scope of this research focused on the differences between vicarious pain responders and non-responders groups that have been matched on age and gender.

5.5 Discussion

5.5.1 Summary of Results

In the present study, we further investigated differences in autonomic and interoceptive processes in vicarious pain responders. We used two different groups of vicarious pain responders, namely the sensory-localised (S/L) group and the affective-general (A/G) group as well as a control group of non-responders. We based our predictions on previous findings in these populations regarding their increased reported sensibility towards their bodies and their higher emotional contagion, but not personal distress and neither anxiety. Firstly, we explored if their increased interoceptive sensibility as previously recorded by MAIA also corresponds to a higher interoceptive accuracy and/or awareness. Secondly, we explored if their increased emotional contagion, together with typical personal distress and anxiety levels, is related to changes in autonomic processes, mainly to regulatory processes manifested in the sympathovagal balance as measured through

HRV. Levels of arousal induced by pain perception were also measured by both SPB and SCR recordings.

Our results indicated that vicarious pain responders do not display higher interoceptive accuracy nor awareness despite their increased sensibility towards bodily changes. Notably, only the A/G group showed lower levels of interoceptive accuracy indicating that they are worse at perceiving their cardiac signals. Anxiety measures reconfirmed previous results indicating that the groups do not differ in neither state nor trait anxiety levels. Moreover, the state of arousal as recorded by SBP and SCR did not indicate higher physiological reactivity in these two groups when compared to controls. There was a significant effect of condition, with injection videos eliciting a more pronounced response, however, this did not differ between groups. Regarding emotion regulation processes, there was a significant higher HRV in the S/L group suggesting that this process may represent a coping mechanism, maintaining typical homeostatic and emotional levels of distress.

More generally, the results support the claim that individual differences in vicarious pain determined, in this instance, by phenomenological reports are linked to individual differences in interoception and autonomic mechanisms. In effect, the differences in interoceptive accuracy (worse in A/G but not S/L) and heartrate variability (greater in S/L than A/G) resembles a neuropsychological double dissociation, albeit within a 'neurotypical' sample. This suggests that these groupings reflect the selective involvement of different mechanisms relevant to vicarious experience.

The main limitations to this study were represented by the small number of pain trials. Moreover, whilst we did check for anxiety, other potentially confounding variables such as depersonalisation, blood-injury-injection phobia (BII), exercise and cardiovascular history which can affect both HR and HRV should have been checked for too (N.B. all participants had normal body mass index (BMI)).

5.5.2 Interoceptive processes

The A/G group has lower interoceptive accuracy when compared to both controls and S/L responders whilst the S/L group has comparable interoceptive accuracy with controls even though both groups of vicarious responders have higher interoceptive sensibility.

Moreover, there were no differences in interoceptive awareness between groups indicating that A/G responders are generally aware of having lower accuracy. This is in line with previous findings suggesting that interoceptive sensitivity and accuracy are dissociable traits (Garfinkel et al., 2015a) and with findings suggesting that interoceptive sensibility as measured with MAIA, is independent from interoceptive accuracy (Cali et al., 2015). The dimension of interoceptive sensibility seems to be connected mainly to the attention paid to our bodies and enhanced in people systematically exposed to or suffering from pain such as chronic pain patients (Valenzuela-Moguillansky et al., 2017), or even vicarious pain responders (Bowling et al., 2019) and not to the actual ability to perceive our cardiac functioning.

The heartbeat counting task (HCT) (Schandry, 1981) used to assess interoceptive accuracy has received some criticism. It has been claimed that non-interoceptive processes such as beliefs about own heart rate influence the performance on the task. Empirical evidence has indicated that enhancing knowledge about one's heart rate through direct feedback increases performance on the task (Ring et al., 2015) and that participants rely on prior estimations of heart rate when reporting the number of heartbeats felt (Desmedt et al., 2018). However, regardless of the strategy used to determine own's heartbeat, it can be assumed that reduced perception of real heartbeats leads to greater reliance on heartbeat estimations. For instance, heartbeat signals are more intense at higher levels of systolic blood pressure resulting in a lower reliance on estimation (O'Brien et al., 1998). It may be that A/G responders have worse "estimations" of their own heartbeat, but this would most likely be related to their poorer perception of the actual heartbeats. Moreover, this fact cannot be attributed to physiological differences in systolic blood pressure since their SBP was not lower and using blood pressure as a covariate did not influence our results ($F(2,63)=4.402$, $p=0.016$, $\eta^2=0.123$, $A/G < C$, $p=0.016$). Another criticism concerns the fact that participants tend to count seconds so, participants with a heartbeat closer to 60 bpm would perform better (Zamariola et al., 2018). Regarding this criticism, measurements of heartbeat rate were introduced in the analysis as a co-variate, the main effect of group being preserved ($F(2,63)=4.717$, $p=0.012$, $\eta^2=0.130$, $A/G < C$, $p=0.010$).

Higher interoceptive accuracy has been associated to lower pain thresholds and arousal levels (Pollatos et al., 2012; Grynberg and Pollatos, 2015), but there is no direct

evidence suggesting that vicarious pain responders have lower pain thresholds when exposed to direct painful stimulation. Moreover, in the present study, it was shown that they do not display higher levels of physiological arousal. Their vicarious pain perception might stem from the ability to simulate it, probably through a top-down process, rather than a bottom-up one. The fact that A/G group displays lower interoceptive accuracy seems to be more related to the fact that lower interoceptive accuracy is linked to a more malleable sense of self associated with depersonalisation-like traits predominant in vicarious pain responders as shown by [Bowling et al. \(2019\)](#). Indeed, abnormal interoceptive processing has been recorded in clinical populations suffering from depersonalisation ([Sedeño et al., 2014](#); [Schulz et al., 2013](#)) but also see [Michal et al. \(2014\)](#)), psychosis ([Ardizzi et al., 2016](#)), and, more generally, abnormal bodily self-consciousness ([Ainley and Tsakiris, 2013](#); [Kunstman et al., 2016](#); [Ferentzi et al., 2018](#)). However, the fact that only the A/G group showed decreased IAcc remains intriguing considering that the S/L group also displays depersonalisation-like traits ([Ferentzi et al., 2018](#)) but also proneness to expand bodily boundaries ([Botan et al., 2018b](#); [Derbyshire et al., 2013](#)). This may suggest that the mechanisms leading to disrupted processing of bodily signals in the A/G group are different from or complementary to the ones leading to dissociable experiences.

A second explanation may reside in their physiology, characterised by a tendency in increased SBP and a propensity towards blood-injury-injection phobia (results collected but not published yet) which may lead to overwhelming and unclear bottom-up cardiac signals. IAcc depends on visceral (i.e. cardiac) afferent signals which are highly affected by external factors including arousing stimuli used in experimental settings ([Eichler and Katkin, 1994](#); [Rief et al., 1998](#)). These stressors usually lead to activation of the sympathetic system and to pronounced afferent signals from the viscera. However, these signals may be confounded and difficult to interpret in the presence of a stressor which may direct attention away from the body ([Chajut and Algom, 2003](#); [Pilgrim et al., 2010](#)). In these regards, there is some evidence that, in conditions of arousal following an experimental stressor, IAcc diminishes in female participants ([Fairclough and Goodwin, 2007](#)). Further evidence suggests that IAcc diminishes under the influence of stressors only if attention ceases to be directed to internal bodily signals and oriented instead towards external stimuli ([Schulz et al., 2013](#)). The IAcc task was always completed at least five minutes

after the experimental task and participants were always instructed to direct attention towards their heart. However, the effects of watching painful videos might have been prolonged in this subgroup, especially if we consider that SBP was high in this group during control videos. Further research addressing the effects of painful stressors on bodily changes as well as their impact over time (e.g. in the next minutes after watching the pain stimuli) may elucidate the cause of lower IAcc in the A/G group.

5.5.3 Anxiety, HRV and Emotion Regulation

Anxiety seems to be positively correlated with interoceptive accuracy (see [Domschke et al. \(2010\)](#) for a review) and neuroimaging studies suggested that the size and reactivity of AI is linked to both heartbeat detection and to general experience of anxiety symptoms ([Paulus and Stein, 2006](#); [Stein et al., 2007](#)). We did not find a correlation in our entire sample between anxiety and IAcc. However, these results should be cautiously considered since our population sample was not representative of the entire population. This is because we deliberately recruited more vicarious pain responders in order to obtain comparable numbers in all three groups. Thus, whilst in the general population the percentage of vicarious responders is about 25, in the present sample it was about 58 (42 participants out of 72 were classed as responders). Importantly, there were no differences in anxiety state nor trait between vicarious pain responders, re-confirming previous results with the same measures ([Bowling et al., 2019](#)), but different to the study of ([Young et al., 2017](#)). In their study, they used a measure of anxiety-sensitivity that focuses on concern in regard to bodily feelings of arousal and their misinterpretation (e.g. 'It scares me when I feel faint', 'When my head is pounding, I worry I could have a stroke' (see [Taylor et al. \(2007\)](#)) as opposed to our use of the STAI which focuses largely on mental states.

Altogether, these specific characteristics of vicarious pain responders including the absence of anxious or distressful traits and the high interoceptive sensibility, but not accuracy ([Botan et al., 2018a](#); [Bowling et al., 2019](#)) indicate that these populations may adopt a mindful approach towards their body. According to the mindful bodily awareness theory proposed by [Mehling et al. \(2012\)](#), increased sensitivity towards bodily signals serves to optimize the integration of internal (e.g. visceral perception) and external sig-

nals (e.g. vicarious pain perception). Due to this, the anxious preoccupation with bodily signals which may occur in painful situations can be avoided. Unfortunately, we cannot establish the directionality of the relation: namely if this general sensibility towards bodily changes leads to higher sensibility towards pain or if it is an adaptive response mediating emotional regulation. However, previous evidence suggests that there is a bidirectional communication between the brain and the body and that top-down processes such as regulation of attention towards the body decrease psychological stress and enhance health and well-being (Taylor et al., 2010; Muehsam et al., 2017).

The fact that vicarious pain perceivers do not have higher levels of anxiety after seeing others in pain may be due to habituation to pain which sometimes is noticed in response to frequent exposure to pain (Bingel et al., 2007) or to the fact that they developed a response mechanism based on mindful interpretation of bodily signals towards occurrence of pain. Indeed, interoceptive sensibility has been associated with better self-regulation capacities (Weiss et al., 2014) and a mindful attitude towards the body was proven to contribute to emotion regulation (Lutz et al., 2013). Based on this, we tested the prediction that vicarious pain responders would have higher emotional regulation as recorded by physiological measures of heart-rate variability.

Emotion regulation, the ability to respond to evocative stimuli in an adaptive manner and in a given situation, critically depends on the adjustment of physiological arousal controlled by the autonomic nervous system (ANS) (Gross, 1998). Heart Rate Variability (HRV) has been used for decades as an index of emotion regulation since it is a measure of the interplay between sympathetic and parasympathetic systems' control over heart rate, thus it indicates the flexibility of the autonomic system crucial for continuous emotional self-regulation (Appelhans and Luecken, 2006). Moreover, it seems to provide a measure of the activation or deactivation of the ANS activity over the heart through branches of the vagal nerve as suggested by both polyvagal (Porges, 2001) and neurovisceral integration (Thayer and Lane, 2000) theories.

Previous research indicated that young people who have higher resting state HRV display lower levels of distress after watching upsetting videos (Fabes et al., 1993) and that they also cope better in social situations (Fabes et al., 1994). A study conducted on mammals, indicated that HRV increases when they are exposed to a painful stimulus, but not to an anxious or both painful and anxious stimulus (Reid et al., 2017). Seemingly,

increased HRV rates in S/L responders may indicate the perception of a painful stimulus as simply pain, without attributing to it a distressful component. Thus, they may use physiological emotion regulation to implement adaptive coping strategies. These results need to be further investigated from a psychological perspective using emotion regulation tasks or questionnaires, the expectation being that they would record better abilities to better regulate, at least when exposed to painful stimuli.

The fact that the A/G group did not show higher HRV despite this group reporting intense sensations of pain not accompanied by anxiety nor distress needs further investigation. It may be that they have another coping mechanism or that their tendency towards BII (at least in part of the participants) attenuated the effect, previous evidence suggesting that HRV is lower in non-clinical panickers and blood phobics (Friedman and Thayer, 1998).

5.5.4 Physiological Arousal: SBP and SCR

Both vicarious pain responders and controls showed elevated SBP and SCR levels in the injection (intense pain) condition providing evidence for physiological arousal in all these groups. Whilst we expected vicarious pain responders to display increased SPB and SCR in the pain condition, we did not expect controls to have a similar response. Moreover, the magnitude of the response in vicarious pain responders was not higher than in controls. There was only a significant condition effect with injection videos eliciting a greater physiological response in all three groups. It is likely that the injection videos elicited sensations such as disgust or fear in non-responders, thus their enhanced arousal response despite not reporting any bodily sensation of pain when watching them (most of them still found them repugnant). A wider variety of pain-eliciting videos that would not necessarily evoke disgust in the observer may capture differences in physiological arousal between responders and non-responders. Regardless of the nature of the stimuli, the physiological arousal observed in all three groups indicates the presence of a bodily response to the sight of pain although only the two vicarious responders consciously report it. In the general population, previous evidence shows that painful images do elicit autonomic responses as measured by both SCR and BP (Vaughan and Lanzetta, 1980; Holand et al., 1999; Hein et al., 2011)) and, at a cortical level, activations

are observed in the neuronal matrix of pain including AI and ACC at the sight of pain without conscious bodily report of it (Jackson et al., 2006; Singer et al., 2004). A mirroring response to pain seems to be ubiquitous and what generally distinguishes vicarious pain responders seems to be the over-activity of this response, at least at a neuronal level (Grice-Jackson et al., 2017a). Enhanced physiological reactivity was not seen in this study in the two groups of vicarious pain responders suggesting that this manifestation is mainly due to top-down mechanisms (e.g. hyperactivity of the somatosensory cortex) rather than bottom-up ones (e.g. disinhibited physiological/visceral response amplifying the vicarious perception). Some evidence suggested that vicarious pain responders may have a hyperreactive autonomic system and be more prone to acute distress (Young et al., 2017) mainly due to a poor regulation of the parasympathetic system (lower HRV and increased HR). Importantly, these results were confounded by anxious traits, namely anxious vicarious pain responders displayed these changes (Nazarewicz et al., 2015) which were not unexpected considering that anxiety has been associated to poorer autonomic regulation and higher physiological arousal (Thayer et al., 1996; Mezzacappa et al., 1996). In our study, we compared these groups exclusively based on their perception of pain and not anxious predispositions and showed that there are no differences in their arousal levels and autonomic reactivity in SCR and SBP.

Discussion

In this final section, the findings reported in this thesis will be summarised and further discussed by assessing the degree to which the empirical research addressed the aims and confirmed or informed the predictions formulated in the introductory chapter. Methodological limitations will also be discussed together with possible improvements to experimental designs and future directions to inform future literature in the field. Lastly, the implications and contributions to the wider literature will be presented in the context of the major theories of vicarious pain perception.

6.1 Summary of Findings

The main aims of this thesis were to explore shared self-other bodily representations in vicarious pain responders by investigating the sense of bodily ownership in these subgroups of the population and to explore affective shared-self other representations by examining empathic traits and physiological processes.

The findings of each empirical chapter addressed the initial aims and partly confirmed the hypotheses as seen in table 6.1. Notably, these findings indicated differences between the two groups of vicarious pain responders in both bodily and affective shared self-other representations. The main differences between the two groups of vicarious pain responders are presented in table 6.2 (N.B. All the results were compared against a baseline measurement represented by the results of the control group, i.e. non-responders).

Table 6.1: The initial aims and findings of each empirical chapter.

Empirical Chapter	Aims	Findings
Article I	To investigate bodily ownership in vicarious pain responders.	The S/L responders but not the A/G responders exhibit increased susceptibility to the RHI in the asynchronous condition only.
Article II	To explain particularities in bodily ownership of vicarious pain responders within current theories of multisensory integration, namely the Bayesian Sensory Inference model.	S/L responders exhibit increased susceptibility to both RHI and EI in the asynchronous condition. S/L responders are more influenced by tactile-temporal predictions.
Article III	To investigate the influence of vicarious pain perception on empathic traits and self-other associations.	Both S/L and A/G responders show heightened emotional reactivity and contagion but not other empathic traits.
Article IV	To explore physiological reactivity in these subgroups and possible coping mechanisms that would contribute to the normal functioning of these individuals.	Evidence for better emotion regulation in the S/L group as measured by HRV but not in the A/G group. A/G responders have lower interoceptive accuracy but not S/L responders.

Table 6.2: The findings for each group when compared to controls in each of the empirical studies conducted.

Study	Sensory-Localised Group	Affective-General Group
Article I	Increased susceptibility to the RHI in the asynchronous and light conditions	-
Article II	Increased susceptibility to the RHI and EI in the asynchronous condition	-
	Rely more on tactile-temporal priors	-
Article III	Enhanced Socially-Elicited Emotional States including Emotional Contagion and Reactivity	Enhanced Socially-Elicited Emotional States including Emotional Contagion and Reactivity
Article IV	-	Lower Interoceptive Accuracy
	Better emotion regulation recorded as HRV	-

In Article I, as hypothesised in the introduction and in line with previous research (see [Derbyshire et al. \(2013\)](#)), vicarious pain responders showed atypical bodily ownership as indicated by their performance on the rubber hand illusion (RHI) paradigm. Importantly, only the S/L group showed increased susceptibility to the RHI and reported significantly higher proprioceptive drift and subjective ratings of ownership and agency than controls in the asynchronous condition. There was also a trend towards higher proprioceptive drift in the light condition (when a laser beam played on the dummy hand) but there were no differences between groups in the other two conditions: touch-only (when only the real hand was stroked) and see-only (when only the dummy hand was stroked) demonstrating that this is not just a general tendency towards incorporating the rubber hand. These findings indicated that the increased susceptibility to the rubber hand illusion as previously recorded by ([Derbyshire et al., 2013](#)) might

have been driven by the S/L group. Moreover, they further distinguished this group as a separate typology amongst other populations that also exhibited particularities in bodily ownership. Compared to mirror-touch synaesthetes (MTS), S/L responders do not report higher ownership in the see-only condition than controls (Davies and White, 2013). Compared to populations characterised by depersonalisation and psychotic traits (Kállai et al., 2015; Germine et al., 2013), the S/L responders do not report higher ratings only in the synchronous condition but also in the asynchronous condition. Their pattern of results is most similar to findings obtained in eating disorders (ED) patients (Eshkevari et al., 2012; Kaplan et al., 2014; Zopf et al., 2016). Following these observations, we screened our vicarious pain responders using the EDE-Q questionnaire (Mond et al., 2006) but we did not obtain a significantly higher prevalence of ED dispositions in the S/L group (results unpublished). Overall, these findings may suggest that both groups have a more unstable bodily phenotype easily modulated by external (environmental) influences, prior beliefs or enhanced visual signals (Vallar and Ronchi, 2009).

In Article II, which represented a follow up of Article I, atypical bodily ownership observed in S/L responders was explored using a second paradigm – the Enfacement Illusion and the atypical susceptibility to the RHI observed in this group was replicated and further investigated within the Bayesian sensory inference model. This model, when applied to the multisensory integration occurring in the RHI, stipulates that a match between expectations and input signals would generate a stronger experience of the illusion and that more precise modalities are weighted more strongly and can override less precise ones (Samad et al., 2015). The model was further addressed in the second study by introducing two conditions: vision-only (i.e. looking at the dummy hand for 2 minutes without any other stimulation) and asynchronous-random (i.e. alternating the strokes between the dummy and the real hand but at unpredictable time intervals). We also took a measure of proprioceptive imprecision, that is the variation within the reports of the ignition position of the real hand without any previous stimulation. The vision-only condition provided information about the strength of visual input in this group; the asynchronous-random condition provided information about their susceptibility to tactile-temporal predictions, and the measure of proprioceptive imprecision provided information about the strength of the incoming proprioceptive signal.

Results showed the following: a) there were no differences between groups in drift

in the vision-only condition indicating that visual input is not more precise in the S/L group; 2) there were no differences in the asynchronous-random condition between groups but results in the asynchronous condition re-confirmed that S/L are more susceptible to the illusion in this condition suggesting that the S/L group relies more on tactile-temporal predictions; 3) there were no differences in proprioceptive imprecision between groups but the magnitude of the imprecision of the proprioceptive signal positively correlated with the magnitude of the drift in the asynchronous and vision-only conditions only in the S/L group indicating that they do not have higher proprioceptive imprecision but they are more susceptible to proprioceptive imprecision than the other two groups. The results obtained in the EI paradigm suggested that S/L responders identify more with the other's face in both synchronous and asynchronous conditions re-confirming that asynchrony is perceived as synchrony in this group and, considering previous results obtained in the RHI, it can be assumed that this is due to the perfect tactile-temporal correlation. Importantly, the EI does not have a proprioceptive component so greater susceptibility to proprioceptive imprecision cannot be applied to the interpretations of these results which are more likely due to tactile-temporal rhythmicity and meeting strong tactile expectations (i.e. receiving the stroke when it is expected). Both EI and RHI explore bodily-ownership by exploiting similar mechanisms of multisensory integration recruiting parietal brain regions such as the intraparietal sulcus (IPS) and the temporo-parietal junction, and the premotor cortex (Ehrsson et al., 2004; Tsakiris et al., 2006; Apps et al., 2013), the main difference residing in the necessity to recall and co-represent facial features when performing the EI, a process recruiting regions such as inferior occipital gyrus (Nagy et al., 2012). Thus, the findings obtained with the RHI by employing the various conditions, could be extrapolated to the EI. However, this should be tested in an EI study using all these conditions and checking if the results are comparable in the synchronous and visual-only conditions in the general population. Altogether, these results suggest that the S/L group employs stronger tactile-temporal priors and rely more on sensory predictions. By generalising to their vicarious trait, it can be assumed that S/L responders have very strong expectations about when and where to experience the physical pain that they observe, thus its immediate and localised characteristics.

Interestingly, proprioceptive drift varies across conditions in the sensory-localised

responders. They report comparable drift in synchronous, asynchronous, vision, and light conditions greater than in the feel-touch, see-touch, or asynchronous random conditions. It would be interesting to further explore all these results which may be interpreted within the Bayesian framework considering the strength of priors and violation of the predictions. Thus, the probability of experiencing the illusion depends on the input signals updating the priors. In the first four conditions, predictions are not violated, and a common cause can be attributed to the experience. In the synchronous condition, touch on both the rubber and dummy hand are felt simultaneously in perfect agreement; in the asynchronous condition, there is a high correlation between touch on the real hand and touch on the dummy hand and the expectation of when and where the touch should be received is met; in the light condition, a tingling and thermal warm sensation is expected and reported by most of the S/L responders; in the visual-only condition, there is no sensory input to violate the expectation that the dummy hand is the real hand. In the last conditions, the expectations are violated or not clearly constructed. In the see-only condition, the expected feeling of touch when touch is seen is never met; in the touch-only condition, the expectation of seeing the touch that is felt on the real hand is never met; finally, in the asynchronous -random condition, no tactile-temporal expectations can be clearly formulated and the touch delivery always has an element of surprise. Overall, it can be concluded that S/L responders rely more on tactile-temporal priors and that their phenomenological experience depends on the probability that these predictions are met (i.e. that their top-down signals are not updated by contradictory bottom-up inputs). By analogy, the multitude of mirror-pain sensations reported in phantom limbs of amputees (Goller et al., 2013) could be attributed to the fact that, without actual bottom-up input from the real limb, it is easier to involuntarily simulate pain in the phantom limb (N.B. they are not congenitally amputees and they have previously experienced the sensation). This pattern of results together with possible directions to be followed to test this hypothesis will be discussed in Section 6.3.

In Article III, shared self-other representation mainly associated with empathic traits were further investigated in vicarious pain responders. This study used subjective measures, namely a series of questionnaires assessing emotional and cognitive empathic abilities and a self-other association task investigated the saliency of the self. The results indicated that both groups of vicarious pain responders scored higher on socially elicited

emotional states (i.e. emotional contagion and reactivity and attitudes towards helping others) but there were no differences in measures of cognitive empathy, personal distress or self-other associations. Between subject analyses and factorial analyses were run to 1) assess differences between groups and 2) explore which empathic traits were highly correlated. The findings showed that vicarious pain responses correspond to a wider trait of general emotional contagion and are not confined exclusively to pain contagion, but there was no evidence supporting the idea that they may have higher levels of empathic understanding and neither personal distress. The empathic traits which were highly correlated and loaded on the same factors indicated that helping attitudes are linked to a helpful rather than avoidant behaviour and that the levels of personal distress are not stimulated by strong emotional responses as previously stated by Bloom (2017) (N.B. only general trait attitudes were recorded in this study and not immediate responses to painful stimulation). Interestingly, personal distress was mainly correlated with cognitive skills rather than emotional reactivity suggesting that, despite high emotional reactivity, cognitive empathic abilities such as perspective taking can moderate the affective responses. Thus, the absence of distress despite increased levels of emotional reactivity in vicarious pain responders may be mediated by their typical social-cognitive skills and better emotion regulation (Bird and Viding, 2014).

Article IV was a follow-up of the third study and further addressed emotional processes in vicarious pain responders by recording physiological changes and interoceptive abilities. This study tested if vicarious pain responders' capacity of enhanced emotional contagion without evidence of personal distress was due to habituation to pain which sometimes is noticed in response to frequent exposure to pain (Bingel et al., 2007) or to the fact that they developed a response mechanism towards occurrence of pain, namely emotional regulation. It also investigated if the increased affective state when witnessing pain corresponded to enhanced physiological reactivity. The study recorded measures of anxiety (both state and trait), emotional regulation (i.e. heart rate variability (HRV)), physiological arousal (i.e. blood pressure and skin conductance response) and detection of internal heart signals (i.e. interoceptive accuracy and awareness). The main findings reconfirmed previous results, namely that the groups did not differ in neither state nor trait anxiety measures and that their physiological arousal as recorded by blood pressure and skin conductance response was not significantly higher than in non-responders. Re-

garding emotion regulation processes, there was a significantly higher HRV in the S/L group whilst observing pain videos suggesting that this process may represent a coping mechanism in this group, maintaining typical homeostatic and emotional levels of distress but, interestingly, it was not higher in the A/G group. Regarding heartbeat perception processes, the A/G group showed lower levels of interoceptive accuracy indicating that they are worse at perceiving their cardiac signals. Overall, these results indicated that individual differences in vicarious pain are linked to differences in cardiac interoceptive and autonomic mechanisms. Moreover, these findings distinguish between the two groups of vicarious pain responders and indicate a selective involvement of different mechanisms relevant to vicarious experience. The fact that S/L responders have higher HRV than non-responders is very likely related to better emotional regulation in this group, however, it is still not clear if they developed this coping mechanisms due to constant indirect experience of pain or if this is a congenital trait. Importantly, emotion regulation seems to be linked to life experiences and follows stages of development with the recruitment of a set of prefrontal brain regions involved in executive function that mature in time (Martin and Ochsner, 2016). Interestingly, the A/G group did not display increased HRV but they still report typical levels of anxiety and personal distress and they did display poorer interoceptive accuracy which has been previously linked to depersonalisation traits (more pronounced in A/G; Bowling et al. (2019)) and anxious traits (Domschke et al., 2010), but they also reported higher interoceptive sensibility as recorded by MAIA (Bowling et al., 2019). Why interoceptive accuracy is lower in this group and why A/G responders do not show higher distress is still unclear and these questions will be addressed in the following section.

6.2 Methodological limitations and future directions

This section will address the methodological limitations encountered in each study as well as suggestions about how to tackle them and future directions based on current findings. Lastly, it will address some general limitations encountered across all studies.

In Articles I and II, the task used, namely the RHI, was robust and previously employed in numerous other studies (Botvinick and Cohen, 1998; Tsakiris and Haggard, 2005; Rohde et al., 2011; Makin et al., 2008). A main limitation of Article II was represen-

ted by the sample size which was considerably smaller than in Article I due to difficulties in recruiting participants. The sample of S/L responders was comparable to the one in article I (about twenty responders), but the number of non-responders was smaller (27 compared to 57 in Article I) whilst the number of A/G responders was limited to twelve. Taking into account medium effect sizes of 0.5 (Field, 2013) and previous research, the initial aim was to recruit at least twenty participants in each group, a target that was achieved for S/L responders and non-responders but not for A/G responders. Importantly, after collapsing proprioceptive drift results from the first and second study for synchronous and asynchronous conditions, the initial results were preserved (see Appendix B.3).

Another limitation of Articles I and II is posed by the possibility that the results could be confounded by other concealed trait differences between the groups such as hypnotisability. A study run on a large sample screened for both vicarious pain experiences and suggestibility traits showed that hypnotisability predicted total pain responses as well as vicarious pain intensity and that the two groups of vicarious pain responders have higher hypnotisability scores (Lush et al., 2019). This is important in the context of RHI studies because previous research indicated that responses to the illusion are influenced by sensory suggestibility (Marotta et al., 2016). The idea that vicarious pain experiences may be linked to imaginative suggestion has been previously vehiculated by De Vignemont and Jacob (2012). The authors suggest that feeling another's pain is intrinsically related to mental imagery and distinguish between empathetic pain as feeling sorry for someone which is in pain and contagious pain as imagining being in pain. According to the authors, vicariously feeling the pain of somebody else consists in choosing to re-enact that pain in a simulation-like fashion. However, it is debatable if it is a deliberate act or not since it is hard to establish if it is purely involuntary (an involuntary reflex) or if the will of the individual is thoroughly manifested in it. They define it as sub-intentional in the sense that it is not an involuntary reflex, but it can occur without conscious awareness of the intention. As such, vicarious responders would have the ability to generate pain-like experiences to meet their expectations of the state, but they would experience it as non-intentional. This is in line with what Ward and Banissy (2015) state as difference between imagined-sensory experience and mirror-sensory experience represented by the lack of sense of self-causation. Future research should address this gap and fully

investigate the link between vicarious pain experiences and imaginative suggestion and to elucidate if vicarious pain experiences are strictly linked to sensory suggestibility (i.e. prior sensory expectancies) or a more general suggestible or imaginary trait. Previous research has indicated that imagery recruits SI activation and that it modulates changes in connectivity between SI and PFC (Ostwald et al., 2012). Future studies should check for possible underlying trait confounds and test the hypothesis that S/L responders rely more on tactile-temporal priors and that their phenomenological experience depends on the probability that these predictions are met (i.e. that their top-down signals are not updated by contradictory bottom-up inputs). This could be achieved by measuring the amplitude signal of somatosensory cortical encoding of Bayesian surprise (Ostwald et al., 2012) possibly in a trial-by-trial RHI paradigm or by delivering electrical tactile stimuli when and where expected or not expected. It would be interesting to also explore the performance and somatosensory cortical responses of S/L responders when the sensorial quality of the stimuli is altered and the touch is delivered either in a congruent condition (soft or rough fabrics are used to touch both the rubber hand and the real hand) or an incongruent 'surprise' condition (different fabrics are used for the rubber hand and real hand respectively).

There is no conclusive information on proprioceptive or somatosensory ability in vicarious pain responders. The measure of proprioceptive imprecision employed in this thesis indicated no significant differences in their proprioceptive ability. More evidence has been obtained in regards to their somatosensory sensibility, but it comes mainly from neuroimaging studies indicating greater activity in the somatosensory cortices (e.g. (Derbyshire et al., 2013; Grice-Jackson et al., 2017a)). Until now, only one behavioural study assessed their ability to detect tactile signals indicating that observing pain equally facilitates the detection of tactile stimuli, both in vicarious pain responders and controls (Vandenbroucke et al., 2014). Tasks assessing tactile/somatosensory sensitivity in vicarious pain responders such as the tactile evaluation kit surface (Darian-Smith and Oke, 1980) and their proprioceptive ability including threshold to detection of passive motion, joint position reproduction, or active movement extent discrimination (Han et al., 2016) could be employed in future research to test for possible differences and their link with performances on bodily ownership paradigms.

In Article III, a variety of questionnaires and a self-other saliency task (Sui et al.,

2012) were used. A total of 125 participants were tested and the initial aim was to recruit at least 30 participants in each group for a medium effect size of 0.5. We recruited 68 non-responders, 37 S/L responders and 21 A/G responders, this group being the least represented in the general population (fewer than 10%) and the hardest to recruit due to reluctance to take part in studies. Significant differences were found in emotional contagion and reactivity between both groups of vicarious responders when compared to non-responders. The other measures did not reach significance and all these results were discussed and interpreted in Article III. Non-significant results obtained with PT measures were the most intriguing since they PT abilities have been previously associated with vicarious pain responses (Derbyshire et al., 2013). Whilst Derbyshire et al. (2013) used an avatar PT task, here the PT subscale of the IRI questionnaire (Davis, 1983) was used. Interestingly, vicarious pain responders did not show increased PT abilities when the director task was previously used (Grice-Jackson, 2018). PT tasks rely mainly on cognitive visual and spatial abilities of the participants in controlled environments whilst self-report measures on their social-understanding and relatedness to others (e.g. 'I try to look at everybody's side of a disagreement before I make a decision'). Further studies are needed to fully understand PT abilities in vicarious pain responders which should include both visual and spatial tasks and subjective reports on a large enough sample, but the focus should be on their spatial perspective and location abilities (e.g. avatar task and possibly RHI task with hands rotated at various degrees) possibly linked to neuronal particularities in the rTPJ (Grice-Jackson et al., 2017b), a region associated with spatial location (Serino et al., 2013). The significant results obtained with emotional contagion should be further investigated with more objective measures of emotion recognition and imitation tasks. Considering embodied mimicry and simulation theories stating that emotional understanding is mediated by mirror simulating mechanisms (Decety and Grèzes, 2006; Gallese, 2003; Niedenthal et al., 2005), we would expect vicarious pain responders to have enhanced embodied mimicry and to perform better on emotion recognition tasks (e.g. ERT, CANTAB, Cambridge Cognition Ltd., 2017) and/or on emotional motor imitation task (Braadbaart et al., 2014) as recorded by reaction times or motor evoked potentials (MEPs) (Schutter et al., 2008).

In Article IV, the main limitations were represented by the lack of a control task for interoceptive testing and the dichotomy of the videos used in the physiological task

(i.e. injections versus falls). The interoceptive accuracy task has been widely criticised (Zamariola et al., 2018; Ring et al., 2015; Desmedt et al., 2018). In future research, this may be overcome by introducing control conditions checking for participants' prior beliefs about their heart rate and/or for participants' tendency to count seconds instead of heartbeats which would lead to a better performance of the participants with a heart-beat closer to 60 bpm. Regarding the nature of the videos used in the main task together with physiological recordings, a specific trend was noticed: injection videos elicited an arousal effect in all groups whilst falls videos did not differ from control videos (there was a trend towards higher BP and SCR in the S/L group only, but it did not reach significance). It is likely that the injection videos elicited sensations such as disgust or fear in non-responders, thus their enhanced arousal response. In future studies, a wider variety of pain-eliciting videos should be used (such as burns, cuts etc.) and more videos of each pain category should be employed for increased study power. Moreover, it will also help distinguish better between the two categories of responders since there is preliminary evidence that A/G responders may have a predisposition to Blood-Injury-Injection (BII) phobia thus their descriptive reports of pain after watching the injection videos. Extra data that has been collected (not published yet) indicated that they score significantly higher on BII questionnaire (Wani et al., 2014) than the other two groups. Thus, future studies should further address the differences between the two groups of vicarious pain responders, with emphasis on the A/G responder group.

There were some general limitations common to all studies. Firstly, the recruitment of participants was difficult due to availability of vicarious pain responders. The VPQ was used for screening most of the students in the School of Psychology who were willing to complete the questionnaire for credits. As such, the samples used in these studies were limited to the undergraduate population of the University of Sussex, most of them being young women. Given the restricted number of vicarious pain responders (less than 25% of the population for both groups), individuals classed as responders were invited through emails to participate in the empirical studies. Because of their limited availability, difficulties in recruiting participants for a follow-up study were often encountered. Consequently, all empirical studies were conducted for a duration of at least two academic years and invitations were sent on a regular basis. This led to the recruitment of considerable larger samples than in previous published studies (e.g. (Osborn

and Derbyshire, 2010; Grice-Jackson et al., 2017a,b; Young et al., 2017; Nazarewicz et al., 2015; Blakemore et al., 2005), but sometimes still not reaching the desired sample size for some of the groups (e.g. A/G group in Article 2) and vicarious pain responder groups being outnumbered by controls.

Another limitation is represented by the fact that female participants are predominant in the samples of the studies presented in this thesis. This is mainly due to the recruitment process which screened undergraduate students from the School of Psychology, where the number of female students is considerably larger than male students. There is some evidence showing that females have increased pain sensitivity than males (for a review, see Bartley and Fillingim (2013) and this may be reflected in the fact that more females report vicarious pain-like responses. However, given the fact that the pool sample was composed mainly from women and that there are no significant gender differences between the groups of responders and non-responders, there is no sufficient evidence to conclude that vicarious pain responses are influenced by gender. Regarding the impact that this fact might have had on the experimental results, whilst there is some evidence showing that the RHI is influenced by individual differences in traits such as suggestibility (Marotta et al., 2016; Lush et al., 2019), kinaesthetic or temporal sensitivity (Costantini et al., 2016) or even empathic traits (Asai et al., 2011), there is no evidence indicating the influence of gender on the RHI. As such, the results obtained in the studies using bodily ownership paradigms are extremely unlikely to be linked to gender differences, especially if we consider that the analyses of comparison were run between groups that were matched for gender and age. Concerning interoceptive measures of accuracy, there is some evidence indicating that females are less efficient in consciously detecting heartbeats, but more in-tune with their bodily sensations (Grabauskaitė et al., 2017). However, when using interoceptive and physiological tasks, the analyses were mainly looking at group comparisons between responders and non-responders which had comparable numbers of males and females as indicated by Chi-square tests. Furthermore, interoceptive accuracy did not show significant effect of gender ($t(68) = -0.918$, $p=0.362$) and, when controlling for gender as a confounder, the results obtained with the interoceptive accuracy task stayed the same ($F(2,66) = 4.760$, $p=0.013$, $\eta^2=0.124$) suggesting that the results obtained are not influenced by gender.

6.3 Contributions to the field and present theories

The first major contribution of this thesis was the refinement of the VPQ. Test-retest reliability analyses were conducted as part of Article I and indicated that the two-step cluster analysis provided more reliable results if intensity was used as an input variable instead of total-pain responses. The use of the intensity variable in the two-step cluster analysis together with the increased number of participants added to the database rendered the measure more conservative. Other measures have been used in the past to assess vicarious experiences, but they lacked detailed questioning on the quality of the pain experienced and the classification of the participants was arbitrary (Osborn and Derbyshire, 2010; Giummarra et al., 2015). Grice-Jackson et al. (2017b) developed an online screening questionnaire which relies on immediate reports of vicarious pain and not just past experiences (compared to Giummarra et al. (2015)) and uses a rigorous classification based on input variables. The classification has become even more conservative following the use of intensity as an input variable and the expansion of the database. As a consequence, the percentages of vicarious pain responders have dropped from 19% to 13% in the case of S/L group and from 12% to 10% in the case of A/G group (the first percentages were reported by Grice-Jackson et al. (2017b), the second percentages were obtained following the last cluster analysis conducted on the most recent database).

A second important contribution to the field was brought by identifying differences in self-other bodily representations in vicarious pain responders and the fact that the atypical susceptibility to bodily ownership paradigms is displayed only by the S/L group. Previous models have suggested that vicarious sensory perception was related to expanded bodily boundaries and self-other bodily confusion (Derbyshire et al., 2013; Davies and White, 2013; Maister et al., 2013). However, these differences were not clearly defined in vicarious pain responders and the explanation was confined to a general tendency to identify more with the other. Our results indicated that this is not just a general tendency but that it is strictly related to tactile experiences and bodily priors. Thus, the increased malleability of bodily ownership in S/L responders occurs only when the expectations about tactile predictions are met. This thesis used for the first time baseline proprioceptive imprecision measures and an asynchronous-random condition and confirmed all testable predictions of the Bayesian Sensory Inference Theory (Samad et al.,

2015) indicating that: a) comparable drift is reported in both synchronous and visual conditions; b) a high tactile-temporal correlation is responsible for the drift observed in the asynchronous condition and c) proprioceptive imprecision is directly correlated to drift amplitude in the visual and asynchronous conditions. Overall, this theory completes previous RHI theories which stated that the susceptibility to the illusion was an interplay of top-down bodily phenomenological expectations and bottom-up incoming multisensory signals (Tsakiris and Haggard, 2005). The Bayesian Sensory Inference theory takes this statement further and seeks to explain the dynamics of this interplay between top-down predictive signals and bottom-up corrective signals. Article II confirmed the predictions of this theory and applied them to the atypical results obtained in the S/L group. Surely, more neurophysiological evidence needs to be collected and the results should be replicated with other paradigms (e.g. EI and entire body-ownership paradigms).

A third important contribution of this thesis consisted in partially unravelling associations between empathetic and affective processes in vicarious pain responders. Previous research has linked vicarious sensory abilities to empathy (Banissy and Ward, 2007; Jackson et al., 2006; Grice-Jackson et al., 2017a), but, at the same time, theories of empathy have repeatedly defined it as a non-unitary construct comprising at least three dimensions: affective (i.e. emotional contagion - a precursor), cognitive (i.e. ToM and PT), and compassion (Bernhardt and Singer, 2012; Bird and Viding, 2014). Indeed, Banissy and Ward (2007) only found significantly higher scores on the emotional reactivity subscale of the Empathy Quotient and not the other two subscales namely social skills and cognitive empathy. Our findings confirmed that vicarious pain responders have higher emotional contagion and regulation but typical cognitive skills and personal distress. These results fitted well within current theories of empathy (Bird and Viding, 2014) indicating that the various dimensions are dissociable and, most importantly, that personal distress can be counteracted by cognitive abilities. Moreover, our findings did not support the claiming that emotional contagion inflicts personal distress and hinders helping attitudes (Bloom, 2017). However, these results do not dismiss Bloom's model, instead they suggest that it should be cautiously considered within the various dimensions that affect empathic behaviours. Interestingly, both groups have higher emotional contagion and reactivity, but only the S/L group displays better emotional regulation. It may be that the A/G group benefits from a different mechanism of emotional control or

that the cognitive awareness constantly distinguishing between self and other may be sufficient to control distress. Of course, these hypotheses need to be further tested.

Finally, this thesis further distinguished between S/L and A/G responders on dimensions of bodily ownership, interoception and emotion regulation. Previous research indicated structural and functional differences in SI between the two groups of vicarious responders (Grice-Jackson et al., 2017a). The research conducted as part of this thesis further differentiated between the two groups demonstrating that better emotional regulation and atypical bodily susceptibility to bodily ownership paradigms such as RHI and EI are only present in the S/L group. Furthermore, the A/G group has lower interoceptive accuracy when compared to controls which may be due to differences in insular activity (Craig, 2002; Critchley et al., 2004; Grice-Jackson et al., 2017a). There are also similarities between the groups, mainly on empathy measures: both groups score higher on emotional contagion and reactivity, but, whilst the S/L group has been characterised by various behavioural, physiological, and neuronal traits, the A/G group profile remains more enigmatic. It has been shown that they have higher emotional reactivity, typical levels of personal distress but not higher emotional regulation and lower interoceptive awareness. All these manifestations may be underlined by neuronal particularities such as increased activity in the affective pain matrix including the anterior insula. Moreover, they do not differ on bodily ownership paradigms and tend to report higher levels of BII. Further research is needed to investigate the profile of the A/G group which seems to be more heterogeneous in its characteristics.

6.4 General Conclusions

This thesis has brought significant contributions to the field of vicarious pain experiences and has further investigated bodily and affective shared self-other representations in two distinct groups of vicarious pain responders. It has broadened our understanding of bodily ownership and emotional processes as well as various aspects of empathy in vicarious pain responders. This research is of theoretical interest in deepening our knowledge on the phenomenon of vicarious pain and its link to broader bodily phenotypes as well as affective processing. It has also paved the way for future research directions and debates regarding the importance of bodily and cognitive distinction between self and

other, the nature of coping mechanisms in response to pain, and inter-individual differences in embodied pain processes. This thesis may also inform future methodological practices and may have implications for improving our understanding of embodiment in vicarious pain.

Bibliography

- Ainley, V. and M. Tsakiris, 2013. Body conscious? interoceptive awareness, measured by heartbeat perception, is negatively correlated with self-objectification. *PloS one* **8**:e55568.
- Alsmith, A., 2015. Mental activity & the sense of ownership. *Review of Philosophy and Psychology* **6**:881–896.
- Appelhans, B. M. and L. J. Luecken, 2006. Heart rate variability as an index of regulated emotional responding. *Review of general psychology* **10**:229–240.
- Appelhans, B. M. and L. J. Luecken, 2008. Heart rate variability and pain: associations of two interrelated homeostatic processes. *Biological psychology* **77.2**:174–182.
- Apps, M. A., A. Tajadura-Jiménez, M. Sereno, O. Blanke, and M. Tsakiris, 2013. Plasticity in unimodal and multimodal brain areas reflects multisensory changes in self-face identification. *Cerebral Cortex* **25**:46–55.
- Ardizzi, M., M. Ambrosecchia, L. Buratta, F. Ferri, M. Peciccia, S. Donnari, C. Mazzeschi, and V. Gallese, 2016. Interoception and positive symptoms in schizophrenia. *Frontiers in human neuroscience* **10**:379.
- Asai, T., Z. Mao, E. Sugimori, and Y. Tanno, 2011. Rubber hand illusion, empathy, and schizotypal experiences in terms of self-other representations. *Consciousness and Cognition* **20**:1744–1750.

- Aspell, J., E. Palluel, and O. Blanke, 2012. Early and late activity in somatosensory cortex reflects changes in bodily self-consciousness: an evoked potential study. *Neuroscience* **216**:110–122.
- Avenanti, A., D. Buetti, G. Galati, and S. M. Aglioti, 2005. Transcranial magnetic stimulation highlights the sensorimotor side of empathy for pain. *Nature neuroscience* **8**:955.
- Avenanti, A., I. Minio-Paluello, A. Sforza, and S. M. Aglioti, 2009. Freezing or escaping? opposite modulations of empathic reactivity to the pain of others. *cortex* **45**:1072–1077.
- Avenanti, A., A. Sirigu, and S. M. Aglioti, 2010. Racial bias reduces empathic sensorimotor resonance with other-race pain. *Current Biology* **20**:1018–1022.
- Bacaër, N., 2011. A short history of mathematical population dynamics. Springer Science & Business Media.
- Banissy, M. J. and J. Ward, 2007. Mirror-touch synesthesia is linked with empathy. *Nature neuroscience* **10**:815.
- Barontini, M., J. O. Lázzari, G. Levin, I. Armando, and S. J. Basso, 1997. Age-related changes in sympathetic activity: biochemical measurements and target organ responses. *Archives of gerontology and geriatrics* **25**:175–186.
- Bartley, E. J. and R. B. Fillingim, 2013. Sex differences in pain: a brief review of clinical and experimental findings. *British journal of anaesthesia* **111**:52–58.
- Batson, C. D., B. D. Duncan, P. Ackerman, T. Buckley, and K. Birch, 1981. Is empathic emotion a source of altruistic motivation? *Journal of personality and Social Psychology* **40**:290.
- Batson, C. D., K. Sager, E. Garst, M. Kang, K. Rubchinsky, and K. Dawson, 1997. Is empathy-induced helping due to self–other merging? *Journal of personality and social psychology* **73**:495.
- Bernhardt, B. C. and T. Singer, 2012. The neural basis of empathy. *Annual review of neuroscience* **35**:1–23.

- Bertamini, M., N. Berselli, C. Bode, R. Lawson, and L. T. Wong, 2011. The rubber hand illusion in a mirror. *Consciousness and cognition* **20**:1108–1119.
- Bingel, U., E. Schoell, W. Herken, C. Büchel, and A. May, 2007. Habituation to painful stimulation involves the antinociceptive system. *Pain* **131**:21–30.
- Bird, G. and E. Viding, 2014. The self to other model of empathy: providing a new framework for understanding empathy impairments in psychopathy, autism, and alexithymia. *Neuroscience & Biobehavioral Reviews* **47**:520–532.
- Blakemore, S.-J., D. Bristow, G. Bird, C. Frith, and J. Ward, 2005. Somatosensory activations during the observation of touch and a case of vision–touch synaesthesia. *Brain* **128**:1571–1583.
- Blanke, O. and T. Metzinger, 2009. Full-body illusions and minimal phenomenal selfhood. *Trends in cognitive sciences* **13**:7–13.
- Bloom, P., 2017. Empathy and its discontents. *Trends in cognitive sciences* **21**:24–31.
- Bolognini, N., C. Miniussi, S. Gallo, and G. Vallar, 2013a. Induction of mirror-touch synaesthesia by increasing somatosensory cortical excitability. *Current Biology* **23**:R436–R437.
- Bolognini, N., A. Rossetti, S. Convento, and G. Vallar, 2013b. Understanding others' feelings: the role of the right primary somatosensory cortex in encoding the affective valence of others' touch. *Journal of Neuroscience* **33**:4201–4205.
- Bornhövd, K., M. Quante, V. Glauche, B. Bromm, C. Weiller, and C. Büchel, 2002. Painful stimuli evoke different stimulus–response functions in the amygdala, prefrontal, insula and somatosensory cortex: a single-trial fmri study. *Brain* **125**:1326–1336.
- Botan, V., N. C. Bowling, M. Banissy, H. Critchley, and J. Ward, 2018a. Individual differences in vicarious pain perception linked to heightened socially elicited emotional states. *Frontiers in psychology* **9**:2355.
- Botan, V., S. Fan, H. Critchley, and J. Ward, 2018b. Atypical susceptibility to the rubber hand illusion linked to sensory-localised vicarious pain perception. *Consciousness and cognition* **60**:62–71.

- Botvinick, M. and J. Cohen, 1998. Rubber hands ‘feel’ touch that eyes see. *Nature* **391**:756.
- Bowling, N. C. and M. J. Banissy, 2017. Modulating vicarious tactile perception with transcranial electrical current stimulation. *European Journal of Neuroscience* **46**:2355–2364.
- Bowling, N. C., V. Botan, I. Santiesteban, J. Ward, and M. J. Banissy, 2019. Atypical bodily self-awareness in vicarious pain responders. *Philosophical Transactions of the Royal Society B* **374**:20180361.
- Braadbaart, L., H. De Grauw, D. Perrett, G. D. Waiter, and J. Williams, 2014. The shared neural basis of empathy and facial imitation accuracy. *NeuroImage* **84**:367–375.
- Bradshaw, J. and J. Mattingley, 2001. Allodynia: a sensory analogue of motor mirror neurons in a hyperaesthetic patient reporting instantaneous discomfort to another’s perceived sudden minor injury? *Journal of Neurology, Neurosurgery & Psychiatry* **70**:135–136.
- Brass, M., S. Zysset, and D. Y. von Cramon, 2001. The inhibition of imitative response tendencies. *Neuroimage* **14**:1416–1423.
- Bucchioni, G., C. Fossataro, A. Cavallo, H. Mouras, M. Neppi-Modona, and F. Garbarini, 2016. Empathy or ownership? evidence from corticospinal excitability modulation during pain observation. *Journal of cognitive neuroscience* **28**:1760–1771.
- Buccino, G., F. Binkofski, and L. Riggio, 2004. The mirror neuron system and action recognition. *Brain and language* **89**:370–376.
- Bufalari, I., T. Aprile, A. Avenanti, F. Di Russo, and S. M. Aglioti, 2007. Empathy for pain and touch in the human somatosensory cortex. *Cerebral Cortex* **17**:2553–2561.
- Bufalari, I., B. Lenggenhager, G. Porciello, B. Serra Holmes, and S. M. Aglioti, 2014. En-facing others but only if they are nice to you. *Frontiers in Behavioral Neuroscience* **8**:102.
- Butz, M. V., E. F. Kutter, and C. Lorenz, 2014. Rubber hand illusion affects joint angle perception. *PLoS One* **9**:e92854.

- Calì, G., E. Ambrosini, L. Picconi, W. Mehling, and G. Committeri, 2015. Investigating the relationship between interoceptive accuracy, interoceptive awareness, and emotional susceptibility. *Frontiers in psychology* **6**:1202.
- Carruthers, G., 2013. Toward a cognitive model of the sense of embodiment in a (rubber) hand. *Journal of Consciousness Studies* **20**:33–60.
- Chajut, E. and D. Algom, 2003. Selective attention improves under stress: implications for theories of social cognition. *Journal of personality and social psychology* **85**:231.
- Cheng, Y., C.-P. Lin, H.-L. Liu, Y.-Y. Hsu, K.-E. Lim, D. Hung, and J. Decety, 2007. Expertise modulates the perception of pain in others. *Current Biology* **17**:1708–1713.
- Coghill, R. C., C. N. Sang, J. M. Maisog, and M. J. Iadarola, 1999. Pain intensity processing within the human brain: a bilateral, distributed mechanism. *Journal of neurophysiology* **82**:1934–1943.
- Cohen, J., 1988. Statistical power analysis for the behavioral sciences. abingdon.
- Costantini, M., 2014. Body perception, awareness, and illusions. *Wiley Interdisciplinary Reviews: Cognitive Science* **5**:551–560.
- Costantini, M. and P. Haggard, 2007. The rubber hand illusion: sensitivity and reference frame for body ownership. *Consciousness and cognition* **16**:229–240.
- Costantini, M., J. Robinson, D. Migliorati, B. Donno, F. Ferri, and G. Northoff, 2016. Temporal limits on rubber hand illusion reflect individuals' temporal resolution in multi-sensory perception. *Cognition* **157**:39–48.
- Craig, A. D., 2002. How do you feel? interoception: the sense of the physiological condition of the body. *Nature reviews neuroscience* **3**:655.
- Craig, A. D. and A. Craig, 2009. How do you feel–now? the anterior insula and human awareness. *Nature reviews neuroscience* **10**.
- Cramer, J. S., 2002. The origins of logistic regression .
- Critchley, H. D., S. Wiens, P. Rotshtein, A. Öhman, and R. J. Dolan, 2004. Neural systems supporting interoceptive awareness. *Nature neuroscience* **7**:189.

- Crucianelli, L., C. Krahé, P. M. Jenkinson, and A. K. Fotopoulou, 2018. Interoceptive ingredients of body ownership: Affective touch and cardiac awareness in the rubber hand illusion. *Cortex* **104**:180–192.
- Darian-Smith, I. and L. E. Oke, 1980. Peripheral neural representation of the spatial frequency of a grating moving across the monkey's finger pad. *The Journal of Physiology* **309**:117–133.
- Davies, A. M. A. and R. C. White, 2013. A sensational illusion: vision-touch synaesthesia and the rubber hand paradigm. *Cortex* **49**:806–818.
- Davis, M. H., 1983. Measuring individual differences in empathy: Evidence for a multi-dimensional approach. *Journal of personality and social psychology* **44**:113.
- Davydov, D. M., D. Shapiro, and I. B. Goldstein, 2010. Relationship of resting baroreflex activity to 24-hour blood pressure and mood in healthy people. *Journal of Psychophysiology*.
- Davydov, D. M., D. Shapiro, I. B. Goldstein, and A. Chicz-DeMet, 2007. Moods in everyday situations: effects of combinations of different arousal-related factors. *Journal of psychosomatic research* **62**:321–329.
- de Guzman, M., G. Bird, M. J. Banissy, and C. Catmur, 2016. Self–other control processes in social cognition: from imitation to empathy. *Philosophical Transactions of the Royal Society B: Biological Sciences* **371**:20150079.
- De Vignemont, F., 2013. The mark of bodily ownership. *Analysis* **73**:643–651.
- De Vignemont, F., 2014. Shared body representations and the 'whose' system. *Neuropsychologia* **55**:128–136.
- De Vignemont, F. and P. Jacob, 2012. What is it like to feel another's pain? *Philosophy of science* **79**:295–316.
- De Vignemont, F. and T. Singer, 2006. The empathic brain: how, when and why? *Trends in cognitive sciences* **10**:435–441.
- Decety, J., 2011. The neuroevolution of empathy. *Annals of the New York Academy of Sciences* **1231**:35–45.

- Decety, J. and J. Grèzes, 2006. The power of simulation: imagining one's own and other's behavior. *Brain research* **1079**:4–14.
- Derbyshire, S. W., J. Osborn, and S. Brown, 2013. Feeling the pain of others is associated with self-other confusion and prior pain experience. *Frontiers in human neuroscience* **7**:470.
- Derbyshire, S. W., M. G. Whalley, and D. A. Oakley, 2009. Fibromyalgia pain and its modulation by hypnotic and non-hypnotic suggestion: An fmri analysis. *European Journal of Pain* **13**:542–550.
- Desmedt, O., O. Luminet, and O. Corneille, 2018. The heartbeat counting task largely involves non-interoceptive processes: Evidence from both the original and an adapted counting task. *Biological Psychology* **138**:185–188.
- Dewe, H., D. G. Watson, and J. J. Braithwaite, 2016. Uncomfortably numb: new evidence for suppressed emotional reactivity in response to body-threats in those predisposed to sub-clinical dissociative experiences. *Cognitive neuropsychiatry* **21**:377–401.
- Doherty, R. W., 1997. The emotional contagion scale: A measure of individual differences. *Journal of nonverbal Behavior* **21**:131–154.
- Domschke, K., S. Stevens, B. Pfleiderer, and A. L. Gerlach, 2010. Interoceptive sensitivity in anxiety and anxiety disorders: an overview and integration of neurobiological findings. *Clinical psychology review* **30**:1–11.
- Durgin, F. H., L. Evans, N. Dunphy, S. Klostermann, and K. Simmons, 2007. Rubber hands feel the touch of light. *Psychological Science* **18**:152–157.
- Ebisch, S. J., M. G. Perrucci, A. Ferretti, C. Del Gratta, G. L. Romani, and V. Gallese, 2008. The sense of touch: embodied simulation in a visuotactile mirroring mechanism for observed animate or inanimate touch. *Journal of cognitive neuroscience* **20**:1611–1623.
- Ehrsson, H. H., C. Spence, and R. E. Passingham, 2004. That's my hand! activity in premotor cortex reflects feeling of ownership of a limb. *Science* **305**:875–877.
- Eichler, S. and E. S. Katkin, 1994. The relationship between cardiovascular reactivity and heartbeat detection. *Psychophysiology* **31**:229–234.

- Eisenberg, N., 2000. Emotion, regulation, and moral development. *Annual review of psychology* **51**:665–697.
- Eisenberger, N. I., M. D. Lieberman, and K. D. Williams, 2003. Does rejection hurt? an fmri study of social exclusion. *Science* **302**:290–292.
- Ernst, M. O. and M. S. Banks, 2002. Humans integrate visual and haptic information in a statistically optimal fashion. *Nature* **415**:429.
- Eshkevari, E., E. Rieger, M. R. Longo, P. Haggard, and J. Treasure, 2012. Increased plasticity of the bodily self in eating disorders. *Psychological Medicine* **42**:819–828.
- Eshkevari, E., E. Rieger, P. Musiat, and J. Treasure, 2014. An investigation of interoceptive sensitivity in eating disorders using a heartbeat detection task and a self-report measure. *European Eating Disorders Review* **22**:383–388.
- Fabes, R. A., N. Eisenberg, and L. Eisenbud, 1993. Behavioral and physiological correlates of children's reactions to others in distress. *Developmental Psychology* **29**:655.
- Fabes, R. A., N. Eisenberg, M. Karbon, D. Troyer, and G. Switzer, 1994. The relations of children's emotion regulation to their vicarious emotional responses and comforting behaviors. *Child development* **65**:1678–1693.
- Fadiga, L., L. Craighero, and E. Olivier, 2005. Human motor cortex excitability during the perception of others' action. *Current opinion in neurobiology* **15**:213–218.
- Fairclough, S. H. and L. Goodwin, 2007. The effect of psychological stress and relaxation on interoceptive accuracy: Implications for symptom perception. *Journal of Psychosomatic Research* **62**:289–295.
- Farmer, H., A. Tajadura-Jiménez, and M. Tsakiris, 2012. Beyond the colour of my skin: How skin colour affects the sense of body-ownership. *Consciousness and cognition* **21**:1242–1256.
- Faul, F., E. Erdfelder, A. Lang, and A. Buchner, 2007. A flexible statistical power analysis program for the social, behavioral and biomedical sciences. *Behavior Research Methods* .

- Fecteau, J. H. and D. P. Munoz, 2006. Salience, relevance, and firing: a priority map for target selection. *Trends in cognitive sciences* **10**:382–390.
- Fedotov, A., 2016. Selection of parameters of bandpass filtering of the ecg signal for heart rhythm monitoring systems. *Biomedical Engineering* **50**:114–118.
- Feinberg, T. E., A. Venneri, A. M. Simone, Y. Fan, and G. Northoff, 2010. The neuroanatomy of asomatognosia and somatoparaphrenia. *Journal of Neurology, Neurosurgery & Psychiatry* **81**:276–281.
- Ferentzi, E., R. Drew, B. T. Tihanyi, and F. Köteles, 2018. Interoceptive accuracy and body awareness—temporal and longitudinal associations in a non-clinical sample. *Physiology & behavior* **184**:100–107.
- Fernández, C., J. C. Pascual, J. Soler, M. Elices, M. J. Portella, and E. Fernández-Abascal, 2012. Physiological responses induced by emotion-eliciting films. *Applied psychophysiology and biofeedback* **37**:73–79.
- Field, A., 2013. Discovering statistics using IBM SPSS statistics. sage.
- Filippetti, M. L., L. P. Kirsch, L. Crucianelli, and A. Fotopoulou, 2019. Affective certainty and congruency of touch modulate the experience of the rubber hand illusion. *Scientific reports* **9**:1–13.
- Fitzgibbon, B. M., P. G. Enticott, A. N. Rich, M. J. Giummarra, N. Georgiou-Karistianis, and J. L. Bradshaw, 2012. Mirror-sensory synaesthesia: exploring ‘shared’ sensory experiences as synaesthesia. *Neuroscience & Biobehavioral Reviews* **36**:645–657.
- Fitzgibbon, B. M., P. G. Enticott, A. N. Rich, M. J. Giummarra, N. Georgiou-Karistianis, J. W. Tsao, S. R. Weeks, and J. L. Bradshaw, 2010a. High incidence of ‘synaesthesia for pain’ in amputees. *Neuropsychologia* **48**:3675–3678.
- Fitzgibbon, B. M., M. J. Giummarra, N. Georgiou-Karistianis, P. G. Enticott, and J. L. Bradshaw, 2010b. Shared pain: from empathy to synaesthesia. *Neuroscience & Biobehavioral Reviews* **34**:500–512.
- Fletcher, P. C. and C. D. Frith, 2009. Perceiving is believing: a bayesian approach to explaining the positive symptoms of schizophrenia. *Nature Reviews Neuroscience* **10**:48.

- Friedman, B. H. and J. F. Thayer, 1998. Anxiety and autonomic flexibility: a cardiovascular approach. *Biological psychology* **47**:243–263.
- Frith, C. D. and U. Frith, 2006. The neural basis of mentalizing. *Neuron* **50**:531–534.
- Fujisaki, W., S. Shimojo, M. Kashino, and S. Nishida, 2004. Recalibration of audiovisual simultaneity. *Nature neuroscience* **7**:773–778.
- Gallese, V., 2003. The roots of empathy: the shared manifold hypothesis and the neural basis of intersubjectivity. *Psychopathology* **36**:171–180.
- Gallese, V. and A. Goldman, 1998. Mirror neurons and the simulation theory of mind-reading. *Trends in cognitive sciences* **2**:493–501.
- Garfinkel, S. N., A. K. Seth, A. B. Barrett, K. Suzuki, and H. D. Critchley, 2015a. Knowing your own heart: distinguishing interoceptive accuracy from interoceptive awareness. *Biological psychology* **104**:65–74.
- Garfinkel, S. N., E. Zorab, N. Navaratnam, M. Engels, N. Mallorquí-Bagué, L. Minati, N. G. Dowell, J. F. Brosschot, J. F. Thayer, and H. D. Critchley, 2015b. Anger in brain and body: The neural and physiological perturbation of decision-making by emotion. *Social cognitive and affective neuroscience* **11**:150–158.
- Gasperin, D., G. Netuveli, J. S. Dias-da Costa, and M. P. Pattussi, 2009. Effect of psychological stress on blood pressure increase: a meta-analysis of cohort studies. *Cadernos de saude publica* **25**:715–726.
- Gavazzeni, J., S. Wiens, and H. Fischer, 2008. Age effects to negative arousal differ for self-report and electrodermal activity. *Psychophysiology* **45**:148–151.
- George, S. Z., E. A. Dannecker, and M. E. Robinson, 2006. Fear of pain, not pain catastrophizing, predicts acute pain intensity, but neither factor predicts tolerance or blood pressure reactivity: An experimental investigation in pain-free individuals. *European Journal of Pain* **10**:457–457.
- Germine, L., T. L. Benson, F. Cohen, and C. I. Hooker, 2013. Psychosis-proneness and the rubber hand illusion of body ownership. *Psychiatry research* **207**:45–52.

- Giummarra, M. J. and J. L. Bradshaw, 2008. Synaesthesia for pain: feeling pain with another. In *Mirror neuron systems*, pages 287–307. Springer.
- Giummarra, M. J., B. Fitzgibbon, N. Georgiou-Karistianis, M. Beukelman, A. Verdejo-Garcia, Z. Blumberg, M. Chou, and S. J. Gibson, 2015. Affective, sensory and empathic sharing of another's pain: The empathy for pain scale. *European Journal of Pain* **19**:807–816.
- Giummarra, M. J., N. Georgiou-Karistianis, S. J. Gibson, M. Chou, and J. L. Bradshaw, 2006. The menacing phantom: What triggers phantom limb pain, and why? In *INTERNATIONAL JOURNAL OF PSYCHOPHYSIOLOGY*, volume 61, pages 354–354. ELSEVIER SCIENCE BV PO BOX 211, 1000 AE AMSTERDAM, NETHERLANDS.
- Goldenberg, G. and H.-O. Karnath, 2006. The neural basis of imitation is body part specific. *Journal of Neuroscience* **26**:6282–6287.
- Goller, A. I., K. Richards, S. Novak, and J. Ward, 2013. Mirror-touch synaesthesia in the phantom limbs of amputees. *Cortex* **49**:243–251.
- Grabauskaitė, A., M. Baranauskas, and I. Griškova-Bulanova, 2017. Interoception and gender: What aspects should we pay attention to? *Consciousness and cognition* **48**:129–137.
- Grice-Jackson, T., 2018. Individual differences in the vicarious perception of pain. Ph.D. thesis, University of Sussex.
- Grice-Jackson, T., H. D. Critchley, M. J. Banissy, and J. Ward, 2017a. Common and distinct neural mechanisms associated with the conscious experience of vicarious pain. *Cortex* **94**:152–163.
- Grice-Jackson, T., H. D. Critchley, M. J. Banissy, and J. Ward, 2017b. Consciously feeling the pain of others reflects atypical functional connectivity between the pain matrix and frontal-parietal regions. *Frontiers in human neuroscience* **11**:507.
- Gross, J. J., 1998. The emerging field of emotion regulation: An integrative review. *Review of general psychology* **2**:271–299.
- Grynberg, D. and O. Pollatos, 2015. Perceiving one's body shapes empathy. *Physiology & behavior* **140**:54–60.

- Gu, X. and S. Han, 2007. Attention and reality constraints on the neural processes of empathy for pain. *Neuroimage* **36**:256–267.
- Haans, A., F. G. Kaiser, D. G. Bouwhuis, and W. A. IJsselstein, 2012. Individual differences in the rubber-hand illusion: Predicting self-reports of people's personal experiences. *Acta psychologica* **141**:169–177.
- Haggard, P., G. D. Iannetti, and M. R. Longo, 2013. Spatial sensory organization and body representation in pain perception. *Current Biology* **23**:R164–R176.
- Hair, J. F., C. M. Ringle, and M. Sarstedt, 2013. Partial least squares structural equation modeling: Rigorous applications, better results and higher acceptance. *Long range planning* **46**:1–12.
- Han, J., G. Waddington, R. Adams, J. Anson, and Y. Liu, 2016. Assessing proprioception: a critical review of methods. *Journal of Sport and Health Science* **5**:80–90.
- Happé, F., J. L. Cook, and G. Bird, 2017. The structure of social cognition: In (ter) dependence of sociocognitive processes. *Annual review of psychology* **68**:243–267.
- Hein, G., C. Lamm, C. Brodbeck, and T. Singer, 2011. Skin conductance response to the pain of others predicts later costly helping. *PloS one* **6**:e22759.
- Hein, G., G. Silani, K. Preuschoff, C. D. Batson, and T. Singer, 2010. Neural responses to ingroup and outgroup members' suffering predict individual differences in costly helping. *Neuron* **68**:149–160.
- Heydrich, L. and O. Blanke, 2013. Distinct illusory own-body perceptions caused by damage to posterior insula and extrastriate cortex. *Brain* **136**:790–803.
- Holand, S., A. Girard, D. Laude, C. Meyer-Bisch, and J.-L. Elghozi, 1999. Effects of an auditory startle stimulus on blood pressure and heart rate in humans. *Journal of hypertension* **17**:1893–1897.
- Holle, H., M. J. Banissy, and J. Ward, 2013. Functional and structural brain differences associated with mirror-touch synaesthesia. *Neuroimage* **83**:1041–1050.

- Holle, H., N. McLatchie, S. Maurer, and J. Ward, 2011. Proprioceptive drift without illusions of ownership for rotated hands in the “rubber hand illusion” paradigm. *Cognitive neuroscience* **2**:171–178.
- Iannetti, G. D., N. P. Hughes, M. C. Lee, and A. Mouraux, 2008. Determinants of laser-evoked eeg responses: pain perception or stimulus saliency? *Journal of neurophysiology* **100**:815–828.
- Iannetti, G. D. and A. Mouraux, 2010. From the neuromatrix to the pain matrix (and back). *Experimental brain research* **205**:1–12.
- Ide, M., 2013. The effect of “anatomical plausibility” of hand angle on the rubber-hand illusion. *Perception* **42**:103–111.
- Ishida, H., K. Suzuki, and L. C. Grandi, 2015. Predictive coding accounts of shared representations in parieto-insular networks. *Neuropsychologia* **70**:442–454.
- Jackson, P. L., E. Brunet, A. N. Meltzoff, and J. Decety, 2006. Empathy examined through the neural mechanisms involved in imagining how i feel versus how you feel pain. *Neuropsychologia* **44**:752–761.
- Jackson, P. L., A. N. Meltzoff, and J. Decety, 2005. How do we perceive the pain of others? a window into the neural processes involved in empathy. *Neuroimage* **24**:771–779.
- Kaiser, H. F., 1974. An index of factorial simplicity. *Psychometrika* **39**:31–36.
- Kállai, J., G. Hegedüs, Á. Feldmann, S. Rózsa, G. Darnai, R. Herold, K. Dorn, P. Kincses, Á. Csathó, and T. Szolcsányi, 2015. Temperament and psychopathological syndromes specific susceptibility for rubber hand illusion. *Psychiatry research* **229**:410–419.
- Kanayama, N., A. Sato, and H. Ohira, 2009. The role of gamma band oscillations and synchrony on rubber hand illusion and crossmodal integration. *Brain and cognition* **69**:19–29.
- Kaplan, R. A., P. G. Enticott, J. Hohwy, D. J. Castle, and S. L. Rossell, 2014. Is body dysmorphic disorder associated with abnormal bodily self-awareness? a study using the rubber hand illusion. *PloS one* **9**:e99981.

- Keyser, C., B. Wicker, V. Gazzola, J.-L. Anton, L. Fogassi, and V. Gallese, 2004. A touching sight: Sii/pv activation during the observation and experience of touch. *Neuron* **42**:335–346.
- Knudsen, E. I., 2007. Fundamental components of attention. *Annu. Rev. Neurosci.* **30**:57–78.
- Koenig, J., A. Loerbroks, M. N. Jarczok, J. E. Fischer, and J. F. Thayer, 2016. Chronic pain and heart rate variability in a cross-sectional occupational sample. *The Clinical journal of pain* **32**:218–225.
- Kunstman, J. W., E. M. Clerkin, K. Palmer, M. T. Peters, D. R. Dodd, and A. R. Smith, 2016. The power within: The experimental manipulation of power interacts with trait bdd symptoms to predict interoceptive accuracy. *Journal of behavior therapy and experimental psychiatry* **50**:178–186.
- Lamm, C., C. D. Batson, and J. Decety, 2007. The neural substrate of human empathy: effects of perspective-taking and cognitive appraisal. *Journal of cognitive neuroscience* **19**:42–58.
- Lamm, C., J. Decety, and T. Singer, 2011. Meta-analytic evidence for common and distinct neural networks associated with directly experienced pain and empathy for pain. *Neuroimage* **54**:2492–2502.
- Landwehr, J. M., 1987. Clustering of large data sets.
- Lenggenhager, B., T. Tadi, T. Metzinger, and O. Blanke, 2007. Video ergo sum: manipulating bodily self-consciousness. *Science* **317**:1096–1099.
- Levenson, R. W. and A. M. Ruef, 1992. Empathy: a physiological substrate. *Journal of personality and social psychology* **63**:234.
- Limanowski, J. and F. Blankenburg, 2015. That’s not quite me: limb ownership encoding in the brain. *Social cognitive and affective neuroscience* **11**:1130–1140.
- Lira, M., J. H. Egito, P. A. Dall’Agnol, D. M. Amodio, Ó. F. Gonçalves, and P. S. Boggio, 2017. The influence of skin colour on the experience of ownership in the rubber hand illusion. *Scientific reports* **7**:15745.

- Lockwood, P. L., 2016. The anatomy of empathy: Vicarious experience and disorders of social cognition. *Behavioural brain research* **311**:255–266.
- Loggia, M. L., M. Juneau, and M. C. Bushnell, 2011. Autonomic responses to heat pain: Heart rate, skin conductance, and their relation to verbal ratings and stimulus intensity. *PAIN®* **152**:592–598.
- Lombardo, M. V., B. Chakrabarti, E. T. Bullmore, S. J. Wheelwright, S. A. Sadek, J. Suckling, M. A. Consortium, and S. Baron-Cohen, 2010. Shared neural circuits for mentalizing about the self and others. *Journal of cognitive neuroscience* **22**:1623–1635.
- Longo, M. R., F. Schüür, M. P. Kammers, M. Tsakiris, and P. Haggard, 2008. What is embodiment? a psychometric approach. *Cognition* **107**:978–998.
- Lush, P., V. Botan, R. B. Scott, A. Seth, J. Ward, and Z. Dienes, 2019. Phenomenological control: response to imaginative suggestion predicts measures of mirror touch synaesthesia, vicarious pain and the rubber hand illusion .
- Lutz, J., U. Herwig, S. Opialla, A. Hittmeyer, L. Jäncke, M. Rufer, M. Grosse Holtforth, and A. B. Brühl, 2013. Mindfulness and emotion regulation—an fmri study. *Social cognitive and affective neuroscience* **9**:776–785.
- Maister, L., M. J. Banissy, and M. Tsakiris, 2013. Mirror-touch synaesthesia changes representations of self-identity. *Neuropsychologia* **51**:802–808.
- Makin, T. R., N. P. Holmes, and H. H. Ehrsson, 2008. On the other hand: dummy hands and peripersonal space. *Behavioural brain research* **191**:1–10.
- Manikandan, S., 2011. Measures of dispersion. *Journal of Pharmacology and Pharmacotherapeutics* **2**:315.
- Marotta, A., M. Tinazzi, C. Cavedini, M. Zampini, and M. Fiorio, 2016. Individual differences in the rubber hand illusion are related to sensory suggestibility. *PloS one* **11**:e0168489.
- Martin, R. E. and K. N. Ochsner, 2016. The neuroscience of emotion regulation development: implications for education. *Current opinion in behavioral sciences* **10**:142–148.

- Matsumoto, D., M. D. Weissman, K. Preston, B. R. Brown, and C. Kupperbusch, 1997. Context-specific measurement of individualism-collectivism on the individual level: The individualism-collectivism interpersonal assessment inventory. *Journal of Cross-Cultural Psychology* **28**:743–767.
- Mazzarella, E., R. Ramsey, M. Conson, and A. Hamilton, 2013. Brain systems for visual perspective taking and action perception. *Social neuroscience* **8**:248–267.
- Meeus, M., D. Goubert, F. De Backer, F. Struyf, L. Hermans, I. Coppieters, I. De Wandele, H. Da Silva, and P. Calders, 2013. Heart rate variability in patients with fibromyalgia and patients with chronic fatigue syndrome: a systematic review. In *Seminars in arthritis and rheumatism*, volume 43, pages 279–287. Elsevier.
- Mehling, W. E., C. Price, J. J. Daubenmier, M. Acree, E. Bartmess, and A. Stewart, 2012. The multidimensional assessment of interoceptive awareness (maia). *PloS one* **7**:e48230.
- Mezzacappa, E., R. E. Tremblay, D. Kindlon, J. P. Saul, L. Arseneault, R. O. Pihl, and F. Earls, 1996. Relationship of aggression and anxiety to autonomic regulation of heart rate variability in adolescent males. *Annals of the New York Academy of Sciences* **794**:376–379.
- Michal, M., B. Reuchlein, J. Adler, I. Reiner, M. E. Beutel, C. Vögele, H. Schächinger, and A. Schulz, 2014. Striking discrepancy of anomalous body experiences with normal interoceptive accuracy in depersonalization-derealization disorder. *PloS one* **9**:e89823.
- Miu, A. C. and F. R. Balteş, 2012. Empathy manipulation impacts music-induced emotions: A psychophysiological study on opera. *PloS one* **7**:e30618.
- Molenberghs, P., H. Johnson, J. D. Henry, and J. B. Mattingley, 2016. Understanding the minds of others: A neuroimaging meta-analysis. *Neuroscience & Biobehavioral Reviews* **65**:276–291.
- Mond, J. M., P. J. Hay, B. Rodgers, and C. Owen, 2006. Eating disorder examination questionnaire (ede-q): norms for young adult women. *Behaviour research and therapy* **44**:53–62.

- Mouraux, A., A. Diukova, M. C. Lee, R. G. Wise, and G. D. Iannetti, 2011. A multisensory investigation of the functional significance of the “pain matrix”. *Neuroimage* **54**:2237–2249.
- Mouraux, A. and G. D. Iannetti, 2009. Nociceptive laser-evoked brain potentials do not reflect nociceptive-specific neural activity. *Journal of neurophysiology* **101**:3258–3269.
- Mu, Y., Y. Fan, L. Mao, and S. Han, 2008. Event-related theta and alpha oscillations mediate empathy for pain. *Brain research* **1234**:128–136.
- Muehsam, D., S. Lutgendorf, P. J. Mills, B. Rickhi, G. Chevalier, N. Bat, D. Chopra, and B. Gurfein, 2017. The embodied mind: a review on functional genomic and neurological correlates of mind-body therapies. *Neuroscience & Biobehavioral Reviews* **73**:165–181.
- Muncer, S. J. and J. Ling, 2006. Psychometric analysis of the empathy quotient (eq) scale. *Personality and Individual differences* **40**:1111–1119.
- Murphy, K. R., B. Myers, and A. Wolach, 2014. Statistical power analysis: A simple and general model for traditional and modern hypothesis tests. Routledge.
- Nagy, K., M. W. Greenlee, and G. Kovács, 2012. The lateral occipital cortex in the face perception network: an effective connectivity study. *Frontiers in psychology* **3**:141.
- Naveteur, J., S. Buisine, and J. H. Gruzelier, 2005. The influence of anxiety on electrodermal responses to distractors. *International Journal of Psychophysiology* **56**:261–269.
- Nazarewicz, J., A. Verdejo-Garcia, and M. J. Giummarra, 2015. Sympathetic pain? a role of poor parasympathetic nervous system engagement in vicarious pain states. *Psychophysiology* **52**:1529–1537.
- Nickell, G. S., 1998. The helping attitude scale. In *106th Annual Convention of the American Psychological Association at San Francisco*.
- Niedenthal, P. M., L. W. Barsalou, P. Winkielman, S. Krauth-Gruber, and F. Ric, 2005. Embodiment in attitudes, social perception, and emotion. *Personality and social psychology review* **9**:184–211.

- Nobusako, S., Y. Nishi, T. Shuto, D. Asano, M. Osumi, and S. Morioka, 2017. Transcranial direct current stimulation of the temporoparietal junction and inferior frontal cortex improves imitation-inhibition and perspective-taking with no effect on the autism-spectrum quotient score. *Frontiers in behavioral neuroscience* **11**:84.
- Northoff, G., P. Qin, and T. E. Feinberg, 2011. Brain imaging of the self-conceptual, anatomical and methodological issues. *Consciousness and cognition* **20**:52–63.
- O'Brien, W. H., G. J. Reid, and K. R. Jones, 1998. Differences in heartbeat awareness among males with higher and lower levels of systolic blood pressure. *International Journal of Psychophysiology* **29**:53–63.
- Osborn, J. and S. W. Derbyshire, 2010. Pain sensation evoked by observing injury in others. *Pain* **148**:268–274.
- Ostwald, D., B. Spitzer, M. Guggenmos, T. T. Schmidt, S. J. Kiebel, and F. Blankenburg, 2012. Evidence for neural encoding of bayesian surprise in human somatosensation. *NeuroImage* **62**:177–188.
- Otsuru, N., A. Hashizume, D. Nakamura, Y. Endo, K. Inui, R. Kakigi, and L. Yuge, 2014. Sensory incongruence leading to hand disownership modulates somatosensory cortical processing. *Cortex* **58**:1–8.
- Palit, S., B. Kuhn, E. Lannon, H. Coleman, M. Payne, L. Chee, K. Thompson, J. Shadlow, and J. Rhudy, 2015. (294) pain anxiety is associated with pain sensitivity even after controlling for anxiety sensitivity. *The Journal of Pain* **16**:S49.
- Pallant, J., 2001. Spss survival manual. maidenhead.
- Palmer, C. J., B. Paton, J. Hohwy, and P. G. Enticott, 2013. Movement under uncertainty: the effects of the rubber-hand illusion vary along the nonclinical autism spectrum. *Neuropsychologia* **51**:1942–1951.
- Parise, C. V., C. Spence, and M. O. Ernst, 2012. When correlation implies causation in multisensory integration. *Current Biology* **22**:46–49.
- Paton, B., J. Hohwy, and P. G. Enticott, 2012. The rubber hand illusion reveals proprioceptive and sensorimotor differences in autism spectrum disorders. *Journal of autism and developmental disorders* **42**:1870–1883.

- Patterson, D. R. and M. P. Jensen, 2003. Hypnosis and clinical pain. *Psychological bulletin* **129**:495.
- Paulus, M. P. and M. B. Stein, 2006. An insular view of anxiety. *Biological psychiatry* **60**:383–387.
- Pezzulo, G., L. Barca, A. L. Bocconi, and A. M. Borghi, 2010. When affordances climb into your mind: advantages of motor simulation in a memory task performed by novice and expert rock climbers. *Brain and Cognition* **73**:68–73.
- Pilgrim, K., M.-F. Marin, and S. J. Lupien, 2010. Attentional orienting toward social stress stimuli predicts increased cortisol responsivity to psychosocial stress irrespective of the early socioeconomic status. *Psychoneuroendocrinology* **35**:588–595.
- Platek, S. M., D. M. Raines, G. G. Gallup Jr, F. B. Mohamed, J. W. Thomson, T. E. Myers, I. S. Panyavin, S. L. Levin, J. A. Davis, L. C. Fonteyn, et al., 2004. Reactions to children's faces: Males are more affected by resemblance than females are, and so are their brains. *Evolution and Human behavior* **25**:394–405.
- Pollatos, O., J. Füstös, and H. D. Critchley, 2012. On the generalised embodiment of pain: how interoceptive sensitivity modulates cutaneous pain perception. *PAIN®* **153**:1680–1686.
- Pollatos, O., K. Gramann, and R. Schandry, 2007. Neural systems connecting interoceptive awareness and feelings. *Human brain mapping* **28**:9–18.
- Porges, S. W., 2001. The polyvagal theory: phylogenetic substrates of a social nervous system. *International journal of psychophysiology* **42**:123–146.
- Preston, C., 2013. The role of distance from the body and distance from the real hand in ownership and disownership during the rubber hand illusion. *Acta psychologica* **142**:177–183.
- Preston, S. D. and F. B. De Waal, 2002. Empathy: Its ultimate and proximate bases. *Behavioral and brain sciences* **25**:1–20.
- Preyde, M., J. Watson, S. Remers, and R. Stuart, 2016. Emotional dysregulation, interoceptive deficits, and treatment outcomes in patients with eating disorders. *Social Work in Mental Health* **14**:227–244.

- Provine, R. R., 1989. Faces as releasers of contagious yawning: An approach to face detection using normal human subjects. *Bulletin of the Psychonomic Society* **27**:211–214.
- Provine, R. R., 1992. Contagious laughter: Laughter is a sufficient stimulus for laughs and smiles. *Bulletin of the Psychonomic Society* **30**:1–4.
- Quattrocki, E. and K. Friston, 2014. Autism, oxytocin and interoception. *Neuroscience & Biobehavioral Reviews* **47**:410–430.
- Reid, K., C. W. Rogers, G. Gronqvist, E. K. Gee, and C. F. Bolwell, 2017. Anxiety and pain in horses measured by heart rate variability and behavior. *Journal of Veterinary Behavior* **22**:1–6.
- Rief, W., W. Hiller, and J. Margraf, 1998. Cognitive aspects of hypochondriasis and the somatization syndrome. *Journal of abnormal psychology* **107**:587.
- Riemer, M., F. Bublatzky, J. Trojan, and G. W. Alpers, 2015. Defensive activation during the rubber hand illusion: Ownership versus proprioceptive drift. *Biological psychology* **109**:86–92.
- Riganello, F., C. Chatelle, C. Schnakers, and S. Laureys, 2019. Heart rate variability as an indicator of nociceptive pain in disorders of consciousness? *Journal of pain and symptom management* **57**:47–56.
- Ring, C., J. Brener, K. Knapp, and J. Mailloux, 2015. Effects of heartbeat feedback on beliefs about heart rate and heartbeat counting: a cautionary tale about interoceptive awareness. *Biological psychology* **104**:193–198.
- Rizzolatti, G., R. Camarda, L. Fogassi, M. Gentilucci, G. Luppino, and M. Matelli, 1988. Functional organization of inferior area 6 in the macaque monkey. *Experimental brain research* **71**:491–507.
- Rizzolatti, G., L. Fogassi, and V. Gallese, 2002. Motor and cognitive functions of the ventral premotor cortex. *Current opinion in neurobiology* **12**:149–154.
- Roberts, R. J. and T. C. Weerts, 1982. Cardiovascular responding during anger and fear imagery. *Psychological Reports* **50**:219–230.

- Rohde, M., M. Di Luca, and M. O. Ernst, 2011. The rubber hand illusion: feeling of ownership and proprioceptive drift do not go hand in hand. *PloS one* **6**:e21659.
- Rollman, G. B., J. Abdel-Shaheed, J. M. Gillespie, and K. S. Jones, 2004. Does past pain influence current pain: biological and psychosocial models of sex differences. *European Journal of Pain* **8**:427–433.
- Rothen, N. and B. Meier, 2013. Why vicarious experience is not an instance of synesthesia. *Frontiers in Human Neuroscience* **7**:128.
- Sacha, J. and W. Pluta, 2005. Different methods of heart rate variability analysis reveal different correlations of heart rate variability spectrum with average heart rate. *Journal of electrocardiology* **38**:47–53.
- Salinas, J., 2017. Mirror touch: Notes from a doctor who can feel your pain.
- Samad, M., A. J. Chung, and L. Shams, 2015. Perception of body ownership is driven by bayesian sensory inference. *PloS one* **10**:e0117178.
- Santiesteban, I., M. J. Banissy, C. Catmur, and G. Bird, 2012. Enhancing social ability by stimulating right temporoparietal junction. *Current Biology* **22**:2274–2277.
- Santiesteban, I., G. Bird, O. Tew, M. C. Cioffi, and M. J. Banissy, 2015. Mirror-touch synaesthesia: Difficulties inhibiting the other. *Cortex* **71**:116–121.
- Sawamoto, N., M. Honda, T. Okada, T. Hanakawa, M. Kanda, H. Fukuyama, J. Konishi, and H. Shibasaki, 2000. Expectation of pain enhances responses to nonpainful somatosensory stimulation in the anterior cingulate cortex and parietal operculum/posterior insula: an event-related functional magnetic resonance imaging study. *Journal of Neuroscience* **20**:7438–7445.
- Schandry, R., 1981. Heart beat perception and emotional experience. *Psychophysiology* **18**:483–488.
- Schmidt, T. T., D. Ostwald, and F. Blankenburg, 2014. Imaging tactile imagery: changes in brain connectivity support perceptual grounding of mental images in primary sensory cortices. *Neuroimage* **98**:216–224.

- Schulz, A., J. Lass-Hennemann, S. Sütterlin, H. Schächinger, and C. Vögele, 2013. Cold pressor stress induces opposite effects on cardioceptive accuracy dependent on assessment paradigm. *Biological psychology* **93**:167–174.
- Schutter, D. J., D. Hofman, and J. Van Honk, 2008. Fearful faces selectively increase corticospinal motor tract excitability: a transcranial magnetic stimulation study. *Psychophysiology* **45**:345–348.
- Schütz-Bosbach, S., P. Tausche, and C. Weiss, 2009. Roughness perception during the rubber hand illusion. *Brain and Cognition* **70**:136–144.
- Schwartz, G. E., D. A. Weinberger, and J. A. Singer, 1981. Cardiovascular differentiation of happiness, sadness, anger, and fear following imagery and exercise. *Psychosomatic medicine* .
- Sedeño, L., B. Couto, M. Melloni, A. Canales-Johnson, A. Yoris, S. Baez, S. Esteves, M. Velásquez, P. Barttfeld, M. Sigman, et al., 2014. How do you feel when you can't feel your body? interoception, functional connectivity and emotional processing in depersonalization-derealization disorder. *PloS one* **9**:e98769.
- Serino, A., A. Alsmith, M. Costantini, A. Mandrigin, A. Tajadura-Jimenez, and C. Lopez, 2013. Bodily ownership and self-location: components of bodily self-consciousness. *Consciousness and cognition* **22**:1239–1252.
- Sforza, A., I. Bufalari, P. Haggard, and S. M. Aglioti, 2010. My face in yours: Visuo-tactile facial stimulation influences sense of identity. *Social neuroscience* **5**:148–162.
- Shaffer, F. and J. Ginsberg, 2017. An overview of heart rate variability metrics and norms. *Frontiers in public health* **5**:258.
- Shimada, S., K. Fukuda, and K. Hiraki, 2009. Rubber hand illusion under delayed visual feedback. *PloS one* **4**:e6185.
- Shimada, S., Y. Qi, and K. Hiraki, 2010. Detection of visual feedback delay in active and passive self-body movements. *Experimental brain research* **201**:359–364.
- Shimada, S., T. Suzuki, N. Yoda, and T. Hayashi, 2014. Relationship between sensitivity to visuotactile temporal discrepancy and the rubber hand illusion. *Neuroscience Research* **85**:33–38.

- Sierra, M., C. Senior, J. Dalton, M. McDonough, A. Bond, M. L. Phillips, A. M. O'Dwyer, and A. S. David, 2002. Autonomic response in depersonalization disorder. *Archives of General Psychiatry* **59**:833–838.
- Silani, G., C. Lamm, C. C. Ruff, and T. Singer, 2013. Right supramarginal gyrus is crucial to overcome emotional egocentricity bias in social judgments. *Journal of neuroscience* **33**:15466–15476.
- Singer, T., H. D. Critchley, and K. Preuschoff, 2009. A common role of insula in feelings, empathy and uncertainty. *Trends in cognitive sciences* **13**:334–340.
- Singer, T. and O. M. Klimecki, 2014. Empathy and compassion. *Current Biology* **24**:R875–R878.
- Singer, T., B. Seymour, J. O'doherty, H. Kaube, R. J. Dolan, and C. D. Frith, 2004. Empathy for pain involves the affective but not sensory components of pain. *Science* **303**:1157–1162.
- Singer, T., B. Seymour, J. P. O'Doherty, K. E. Stephan, R. J. Dolan, and C. D. Frith, 2006. Empathic neural responses are modulated by the perceived fairness of others. *Nature* **439**:466.
- Sowden, S., G. R. Wright, M. J. Banissy, C. Catmur, and G. Bird, 2015. Transcranial current stimulation of the temporoparietal junction improves lie detection. *Current Biology* **25**:2447–2451.
- Spielberger, C., R. Gorsuch, R. Lushene, P. Vagg, and G. Jacobs, 1983. Manual for the state-trait anxiety scale. *Consulting Psychologists* .
- Stein, M. B., A. N. Simmons, J. S. Feinstein, and M. P. Paulus, 2007. Increased amygdala and insula activation during emotion processing in anxiety-prone subjects. *American Journal of Psychiatry* **164**:318–327.
- Strigo, I. A., S. C. Matthews, A. N. Simmons, T. Oberndorfer, M. Klabunde, L. E. Re-inhardt, and W. H. Kaye, 2013. Altered insula activation during pain anticipation in individuals recovered from anorexia nervosa: evidence of interoceptive dysregulation. *International Journal of Eating Disorders* **46**:23–33.

- Sui, J., X. He, and G. W. Humphreys, 2012. Perceptual effects of social salience: evidence from self-prioritization effects on perceptual matching. *Journal of Experimental Psychology: Human perception and performance* **38**:1105.
- Sui, J., M. Liu, C. Mevorach, and G. W. Humphreys, 2013a. The salient self: The left intraparietal sulcus responds to social as well as perceptual-salience after self-association. *Cerebral Cortex* **25**:1060–1068.
- Sui, J., P. Rotshtein, and G. W. Humphreys, 2013b. Coupling social attention to the self forms a network for personal significance. *Proceedings of the National Academy of Sciences* **110**:7607–7612.
- Tajadura-Jimenez, A., S. Grehl, and M. Tsakiris, 2011. The other in me: Interpersonal multisensory stimulation changes the mental representation of the self. *i-Perception* **2**:963–963.
- Taylor, A. G., L. E. Goehler, D. I. Galper, K. E. Innes, and C. Bourguignon, 2010. Top-down and bottom-up mechanisms in mind-body medicine: development of an integrative framework for psychophysiological research. *Explore* **6**:29–41.
- Taylor, S., M. J. Zvolensky, B. J. Cox, B. Deacon, R. G. Heimberg, D. R. Ledley, J. S. Abramowitz, R. M. Holaway, B. Sandin, S. H. Stewart, et al., 2007. Robust dimensions of anxiety sensitivity: development and initial validation of the anxiety sensitivity index-3. *Psychological assessment* **19**:176.
- Thakkar, K. N., H. S. Nichols, L. G. McIntosh, and S. Park, 2011. Disturbances in body ownership in schizophrenia: evidence from the rubber hand illusion and case study of a spontaneous out-of-body experience. *PloS one* **6**:e27089.
- Thayer, J. F., F. Åhs, M. Fredrikson, J. J. Sollers III, and T. D. Wager, 2012. A meta-analysis of heart rate variability and neuroimaging studies: implications for heart rate variability as a marker of stress and health. *Neuroscience & Biobehavioral Reviews* **36**:747–756.
- Thayer, J. F., B. H. Friedman, and T. D. Borkovec, 1996. Autonomic characteristics of generalized anxiety disorder and worry. *Biological psychiatry* **39**:255–266.

- Thayer, J. F. and R. D. Lane, 2000. A model of neurovisceral integration in emotion regulation and dysregulation. *Journal of affective disorders* **61**:201–216.
- Thompson, R. A., 1991. Emotional regulation and emotional development. *Educational Psychology Review* **3**:269–307.
- Tone, E. B. and E. C. Tully, 2014. Empathy as a “risky strength”: A multilevel examination of empathy and risk for internalizing disorders. *Development and psychopathology* **26**:1547–1565.
- Tracy, L. M., L. Ioannou, K. S. Baker, S. J. Gibson, N. Georgiou-Karistianis, and M. J. Giummarra, 2016. Meta-analytic evidence for decreased heart rate variability in chronic pain implicating parasympathetic nervous system dysregulation. *Pain* **157**:7–29.
- Tracy, L. M., J. Koenig, N. Georgiou-Karistianis, S. J. Gibson, and M. J. Giummarra, 2018. Heart rate variability is associated with thermal heat pain threshold in males, but not females. *International journal of psychophysiology* **131**:37–43.
- Treede, R.-D., 2003. Neurophysiological studies of pain pathways in peripheral and central nervous system disorders. *Journal of neurology* **250**:1152–1161.
- Tsakiris, M., 2008. Looking for myself: current multisensory input alters self-face recognition. *PloS one* **3**:e4040.
- Tsakiris, M., 2010. My body in the brain: a neurocognitive model of body-ownership. *Neuropsychologia* **48**:703–712.
- Tsakiris, M., 2017. The multisensory basis of the self: from body to identity to others. *The Quarterly Journal of Experimental Psychology* **70**:597–609.
- Tsakiris, M., M. Costantini, and P. Haggard, 2008. The role of the right temporo-parietal junction in maintaining a coherent sense of one’s body. *Neuropsychologia* **46**:3014–3018.
- Tsakiris, M. and P. Haggard, 2005. The rubber hand illusion revisited: visuotactile integration and self-attribution. *Journal of Experimental Psychology: Human Perception and Performance* **31**:80.

- Tsakiris, M., A. T. Jiménez, and M. Costantini, 2011. Just a heartbeat away from one's body: interoceptive sensitivity predicts malleability of body-representations. *Proceedings of the Royal Society B: Biological Sciences* **278**:2470–2476.
- Tsakiris, M., G. Prabhu, and P. Haggard, 2006. Having a body versus moving your body: How agency structures body-ownership. *Consciousness and cognition* **15**:423–432.
- Vachon-Presseau, E., M. Roy, M.-O. Martel, E. Caron, M.-F. Marin, J. Chen, G. Albouy, I. Plante, M. J. Sullivan, S. J. Lupien, et al., 2013. The stress model of chronic pain: evidence from basal cortisol and hippocampal structure and function in humans. *Brain* **136**:815–827.
- Valenzuela-Moguillansky, C., A. Reyes-Reyes, and M. I. Gaete, 2017. Exteroceptive and interoceptive body-self awareness in fibromyalgia patients. *Frontiers in human neuroscience* **11**:117.
- Vallar, G. and R. Ronchi, 2009. Somatoparaphrenia: a body delusion. a review of the neuropsychological literature. *Experimental brain research* **192**:533–551.
- Van de Cruys, S., K. Evers, R. Van der Hallen, L. Van Eylen, B. Boets, L. de Wit, and J. Wagemans, 2014. Precise minds in uncertain worlds: Predictive coding in autism. *Psychological review* **121**:649.
- Vandenbroucke, S., G. Crombez, T. Loeys, and L. Goubert, 2014. Observing another in pain facilitates vicarious experiences and modulates somatosensory experiences. *Frontiers in human neuroscience* **8**:631.
- Vaughan, K. B. and J. T. Lanzetta, 1980. Vicarious instigation and conditioning of facial expressive and autonomic responses to a model's expressive display of pain. *Journal of personality and social psychology* **38**:909.
- Vaughan, K. B. and J. T. Lanzetta, 1981. The effect of modification of expressive displays on vicarious emotional arousal. *Journal of Experimental Social Psychology* **17**:16–30.
- Vul, E., C. Harris, P. Winkielman, and H. Pashler, 2009. Puzzlingly high correlations in fmri studies of emotion, personality, and social cognition. *Perspectives on psychological science* **4**:274–290.

- Wani, A. L., A. Ara, and S. A. Bhat, 2014. Blood injury and injection phobia: the neglected one. *Behavioural neurology* **2014**.
- Ward, J. and M. J. Banissy, 2015. Explaining mirror-touch synesthesia. *Cognitive Neuroscience* **6**:118–133.
- Ward, J., V. Burckhardt, and H. Holle, 2013. Contagious scratching: shared feelings but not shared body locations. *Frontiers in human neuroscience* **7**:122.
- Ward, J., P. Schnakenberg, and M. J. Banissy, 2018. The relationship between mirror-touch synaesthesia and empathy: New evidence and a new screening tool. *Cognitive neuropsychology* **35**:314–332.
- Ward Jr, J. H., 1963. Hierarchical grouping to optimize an objective function. *Journal of the American statistical association* **58**:236–244.
- Weiss, S., M. Sack, P. Henningsen, and O. Pollatos, 2014. On the interaction of self-regulation, interoception and pain perception. *Psychopathology* **47**:377–382.
- Yim, O. and K. T. Ramdeen, 2015. Hierarchical cluster analysis: comparison of three linkage measures and application to psychological data. *The quantitative methods for psychology* **11**:8–21.
- Young, K. A., S. C. Gandevia, and M. J. Giummarra, 2017. Vicarious pain responders and emotion: Evidence for distress rather than mimicry. *Psychophysiology* **54**:1081–1095.
- Zamariola, G., P. Maurage, O. Luminet, and O. Corneille, 2018. Interoceptive accuracy scores from the heartbeat counting task are problematic: Evidence from simple bivariate correlations. *Biological psychology* **137**:12–17.
- Zeller, D., K. J. Friston, and J. Classen, 2016. Dynamic causal modeling of touch-evoked potentials in the rubber hand illusion. *Neuroimage* **138**:266–273.
- Zopf, R., E. Contini, C. Fowler, N. Mondraty, and M. A. Williams, 2016. Body distortions in anorexia nervosa: Evidence for changed processing of multisensory bodily signals. *Psychiatry research* **245**:473–481.
- Zusman, M., 2002. Forebrain-mediated sensitization of central pain pathways: ‘non-specific’ pain and a new image for mt. *Manual therapy* **7**:80–88.

Appendix A: Supplementary Materials for Article I

A.1 VPQ group differences comparing TPRs with intensity

Table A.1: Number of subjects in each group for test and post-test generated with TPR or Intensity as cluster analysis variables.

Group	Time 1		Time 2		Entire Sample	
	TPR	Intensity	TPR	Intensity	TPR	Intensity
Controls	49	49	51	55	73 ⁰	773
S/L	21	21	18	17	191	158
A/G	12	12	13	10	135	125

Overall, 2 subjects changed group at time 1 when comparing TPR with Intensity representing 2.44% of the sample (N=82) and 4 subjects changed group at time 2 representing 4.88%.

At the entire sample level (N=1056), 48 subjects changed group, representing 4.5%.

A.2 Baseline comparisons and non-parametric tests

Further one sample t-tests were conducted for a comparison to a baseline of 'o' for all groups and all conditions. Significant results were obtained in controls for synchronous condition, $t(53) = 4.632$, $p < 0.001$; in S/L for synchronous, $t(20) = 4.112$, $p = 0.001$, asynchronous $t(20) = 4.295$, $p < 0.001$ and **light $t(20) = 2.528$, $p = 0.02$** ; in A/G for synchronous $t(18) = 5.18$, $p < 0.001$.

Table A.2: Means and standard deviations for light subjective ratings according to the presence of light induced sensation.

Light Subscale	Sensations present	Sensations Absent
Ownership	3.7 ± 1.42	2.31 ± 1.27
Location	4.00 ± 1.46	2.20 ± 1.21
Agency	3.23 ± 1.46	1.71 ± 0.94

Independent Sample t-tests showed that there was a significant difference in subjective ratings of illusion strength in the light condition between those who did report light-induced sensations and those who did not. Higher subjective ratings were found for light ownership $t(39) = 3.229$, $p < 0.05$; light location $t(39) = 4.162$, $p < 0.001$; light agency $t(39) = 3.780$, $p < 0.001$. Non-parametric Mann-Whitney U test confirmed these results.

A.3 Percentages of people experiencing the illusion in each group

Table A.3: Percentages of subjects experiencing the illusion in each group, namely participants who reported a **positive proprioceptive drift**.

Group	Synchronous	Asynchronous	Light	See-touch	Feel-touch
Controls	72	53	54	39	40
Sensory-localised	86	82	77	59	36
Affective-general	89	26	42	58	53

Table A.4: Percentages of subjects experiencing the illusion for each subscale of each condition, namely participants whose score was higher than 4.

	Syn			Asyn			Light			See			Feel		
	Own	Loc	Age	Own	Loc	Age	Own	Loc	Age	Own	Loc	Age	Own	Loc	Age
C	53	44	35	16	19	16	23	18	19	16	18	14	19	16	14
S/L	73	77	59	32	27	32	50	45	32	27	32	23	27	27	27
A/G	68	68	37	11	21	0	32	37	16	21	26	11	16	21	5

Table A.5: Percentages of subjects who scored **higher than 4** for at least one of the subscales.

Group	Synchronous	Asynchronous	Light	See-touch	Feel-touch
Controls	60	25	32	25	25
Sensory-localised	86	45	64	41	36
Affective-general	74	21	47	42	21

Appendix B: Supplementary Materials for Article II

B.1 RHI and EI questionnaire items

Table B.1: RHI Questionnaire. Items and Subscales.

Subscale	Items
Ownership	<i>It seemed like...</i>
	1. ...I was looking directly at my own hand, rather than at a rubber hand.
	2. ...the rubber hand began to resemble my real hand.
	3. ...the rubber hand belonged to me.
	4. ...the rubber hand was my hand.
	5. ...the rubber hand was part of my body.
Location	6. ...my hand was in the location where the rubber hand was.
	7. ...the rubber hand was in the location where my hand was.
	8. ...the sensation I felt was caused by the paintbrush touching (or laser pointer playing on) the rubber hand.
Agency	9. ...I could have moved the rubber hand if I had wanted.
	10. ...I was in control of the rubber hand.

B.2 RHI entire sample analyses

B.2.1 Proprioceptive drift results

Differences between conditions were compared in the entire sample in a repeated measures ANOVA; sphericity was assumed, and Bonferroni adjustments were applied. There

Table B.2: EI Questionnaire. Items and Subscales.

Subscale	Items
Ownership	<i>It seemed like...</i>
	1. I felt the touch delivered in the other's face.
	2. The touch I felt was caused by the cotton bud touching the other's face.
	3. The other's face was my face.
	4. The other's face was part of my body.
Appearance	5. The other's face belonged to me.
	6. I was looking at my own reflection in a mirror rather than at the other's face.
	7. The other's face began to resemble my own face in terms of shape.
	8. The other's face began to resemble my own face in terms of skin tone.
Agency	9. The other's face began to resemble my own face in terms of facial features.
	10. The other's face would have moved if I had moved.
	11. I was in control of the other's face.
Disownership	12. My own face was out of my control.
	13. I couldn't really remember how my face was.
	14. The experience of my own face was less vivid than normal.

were significant differences between conditions $F(3,123) = 6.043$, $p=0.001$. Pairwise comparisons indicated that drift in the synchronous condition was significantly higher than drift in the asynchronous-random condition, $p=0.002$, but not than the visual-only, $p=1.000$, and asynchronous, $p=0.182$, conditions. Drift in the vision-only condition was higher than in the asynchronous-random, $p=0.026$, but not than in the asynchronous condition, $p=0.921$.

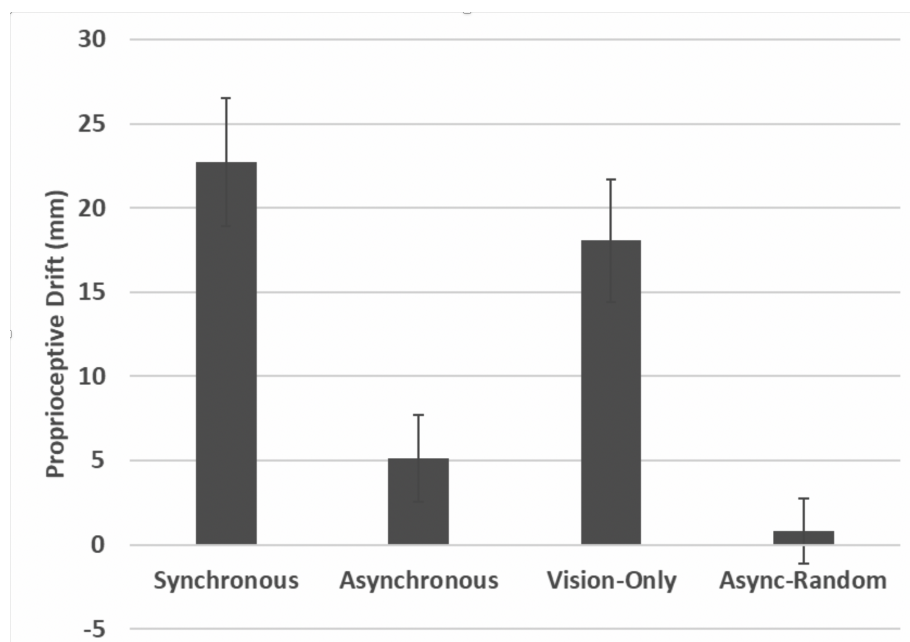


Figure B.1: The drift in each of the four conditions obtained on the entire sample.

B.2.2 Questionnaire results

Ownership

Non-parametric Friedman test indicated that there were significant differences between conditions, $\chi^2 = 56.705, p < 0.001$. Post-hoc Wilcoxon tests indicate that feelings of ownership were greater in the synchronous condition than in all other conditions: asynchronous, $Z = -6.412, p < 0.001$; visual, $Z = -5.892, p < 0.001$; asynchronous-random, $Z = -5.739, p < 0.001$. Feelings of ownership in the visual condition were greater than in the asynchronous condition, $Z = -2.199, p = 0.028$ but not than in the asynchronous random condition, $Z = -1.125, p = 0.261$. Ratings in the asynchronous random and asynchronous were comparable: $Z = -0.942, p = 0.346$.

Location

Non-parametric Friedman test indicated that there were significant differences between conditions, $\chi^2 = 50.466, p < 0.001$. Post-hoc Wilcoxon tests indicate that perceived location was greater in the synchronous condition than in all other conditions: asynchronous, $Z = -5.862, p < 0.001$; visual, $Z = -5.781, p < 0.001$; asynchronous-random, $Z = -5.387, p < 0.001$. Perceived location in the visual condition did not differ from the asynchronous condition, $Z = -0.615, p = 0.539$ nor asynchronous-random condition, $Z = -0.775, p = 0.439$. Location ratings in the asynchronous random and asynchronous were comparable: $Z = -0.364, p = 0.716$.

Agency

Non-parametric Friedman test indicated that there were significant differences between conditions, $\chi^2 = 88.101, p < 0.001$. Post-hoc Wilcoxon tests indicate that feelings of agency were greater in the synchronous condition than in all other conditions: asynchronous, $Z = -5.311, p < 0.001$; visual, $Z = -6.587, p < 0.001$; asynchronous-random, $Z = -4.700, p < 0.001$. Feelings of agency in the visual condition were greater than in the asynchronous condition, $Z = -4.197, p < 0.001$ and asynchronous-random condition, $Z = -4.858, p < 0.001$. Ratings in the asynchronous random and asynchronous were comparable: $Z = -0.779, p = 0.436$.

N.B. The entire sample analyses are confounded by the fact that the proportion of vicarious pain responders, mainly S/L responders, was much higher than in a randomly selected sample, 54% compared to 27%.

B.2.3 Correlation analyses between drift and subjective ratings

Table B.3: Correlation results between drift in each condition and questionnaire subscales.

	Syn			Asyn			Vis			Asyn Rand		
	Own	Loc	Age	Own	Loc	Age	Own	Loc	Age	Own	Loc	Age
Syn Drift	r=0.084 p=0.529	r=0.147 p=0.270	r=0.141 p=0.239									
Asyn Drift				r=0.306 p=0.020	r=0.336 p=0.010	r=0.326 p=0.012						
Vis Drift							r= 0.269 p= 0.043	r=0.209 p=0.111	r=0.370 p=0.005			
Asyn Rand Drift										r=0.224 p=0.139	r=0.107 p=0.484	r=-0.118 p=0.439

As Table B.3 shows, correlations between proprioceptive drift and questionnaire results were obtained only for the asynchronous and vision-only conditions.

B.2.4 Differences in proprioceptive imprecision depending on the preceding condition

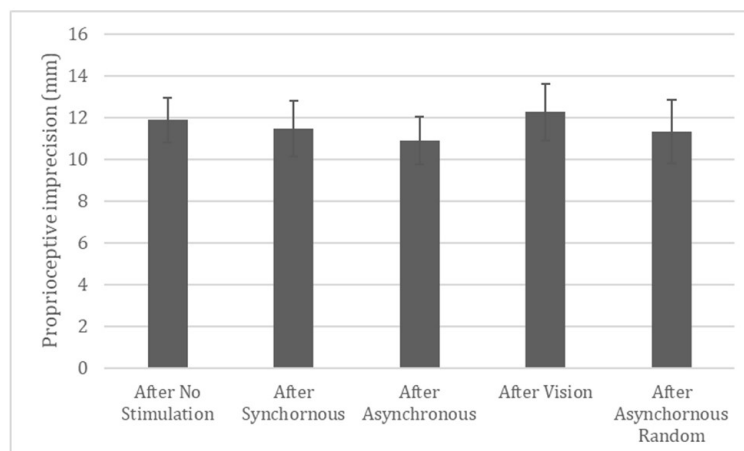


Figure B.2: Differences in proprioceptive imprecision based on the preceding condition.

There were no significant differences between conditions ($F(3.369,171.805) = 0.327$, $p = 0.828$, $\eta^2 = 0.006$) and accounting for group interaction did not influence these results ($F(6.760,165.613) = 0.561$, $p = 0.781$, $\eta^2 = 0.022$). Furthermore, the conditions did not predict the magnitude of proprioceptive imprecision, not even when accounting for group interaction. The regression model using conditions as predictors only accounted for 0.6% of the variation and it was not significant ($F(1,206) = 0.008$, $p = 0.930$).

B.3 Collapsing results for drift in the synchronous and asynchronous conditions

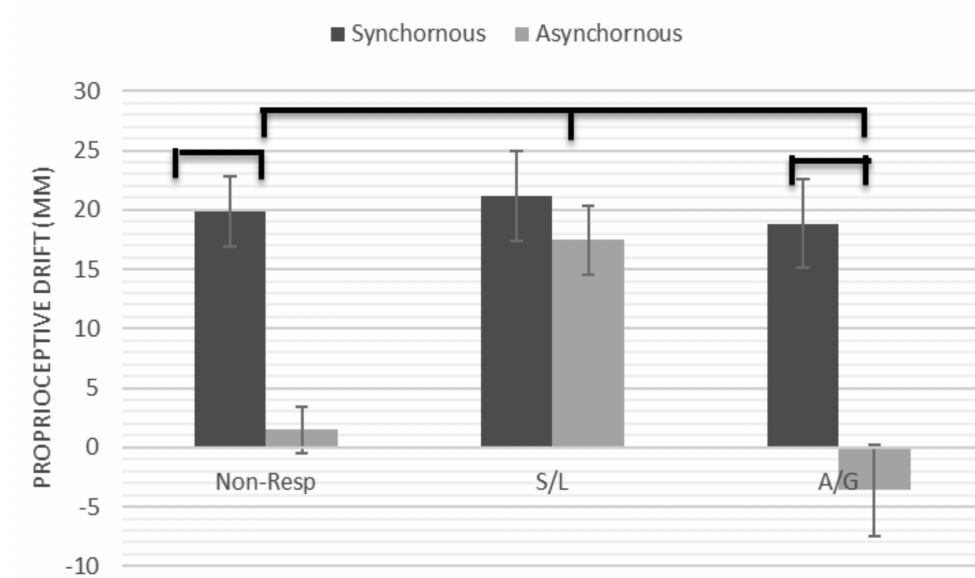


Figure B.3: The results collapsed across the two studies using RHI in vicarious pain responders. The final sample size was: controls, $N = 84$; S/L, $N = 41$; A/G, $N = 31$.

Appendix C: Supplementary Materials for Article III

C.1 Non-parametric tests results.

Kruskal-Wallis H test for measures that were not normally distributed re-confirmed the parametric test results regarding differences between groups: EQ-C ($\chi^2 = 5.061, p = 0.080$), IRI-EC ($\chi^2 = 4.698, p = 0.095$), ICIAI family ($\chi^2 = 0.710, p = 0.701$) and colleagues ($\chi^2 = 1.284, p = 0.526$).

C.2 Effect sizes

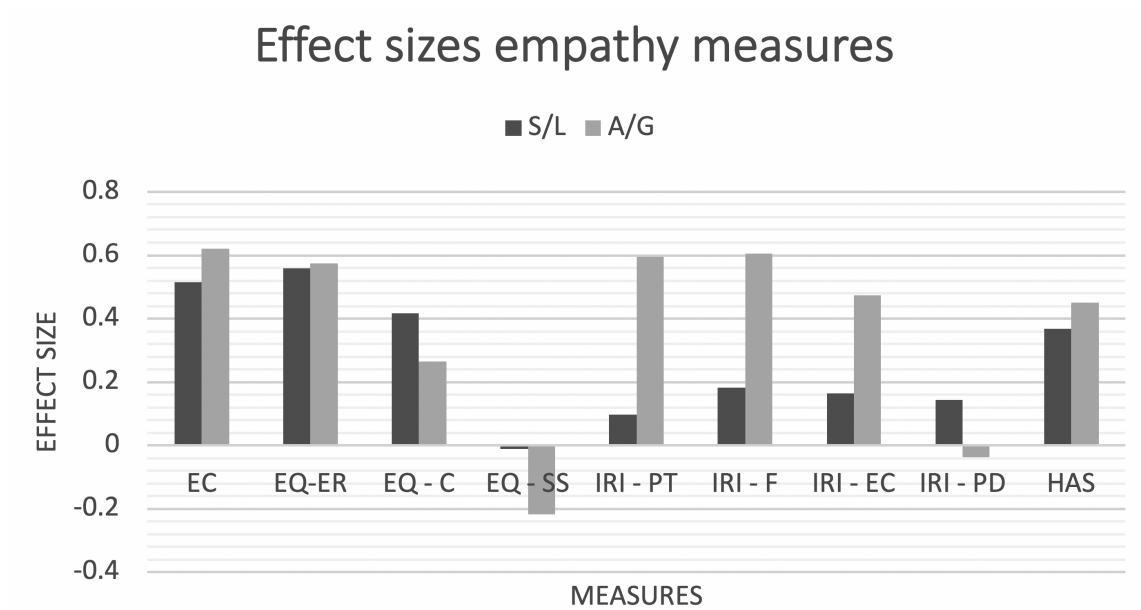


Figure C.1: Effect sizes for EC, EQ subscales, IRI subscales and HAS for S/L and A/G when compared to controls. Medium effect sizes (Cohen's $d > 0.5$) were observed on EC and EQ-ER for both S/L and A/G and on IRI-PT and IRI-F only for A/G. All the other effect sizes were small.

Appendix D: Supplementary Materials for Article IV

D.1 Non-parametric tests results

Interoceptive Accuracy: There were significant group differences: ($H(2) = 14.729, p = 0.001$), $A/G < C$ ($U = -3.737, p < 0.001$) and $A/G < S/L$ ($U = -3.006, p = 0.002$). Task HR: There was main effect of condition ($\chi^2(2) = 94.645, p < 0.001$). There were no group differences for neither of the conditions: control videos ($H(2) = 0.549, p = 0.760$); accident videos ($H(2) = 0.179, p = 0.914$); injection videos ($H(2) = 0.626, p = 0.731$). Task SCR: There was main effect of condition ($\chi^2(2) = 23.495, p < 0.001$). There were no group differences for neither of the conditions: control videos ($H(2) = 0.483, p = 0.786$); accident videos ($H(2) = 0.328, p = 0.849$); injection videos ($H(2) = 0.132, p = 0.936$).